A quantitative assessment of variation in Holocene Khoesan crania from South Africa's western, south-western, southern and south-eastern coasts and coastal forelands

by

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ABSTRACT OF THE THESIS

A quantitative assessment of variation in Holocene Khoesan crania from South Africa's western, south-western, southern and south-eastern coasts and coastal forelands

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It is becoming increasingly evident that the patterns of craniofacial morphology exhibited by several recent human populations around the world, post-date the Pleistocene. While there is an abundance of data available on the origins of recent human craniofacial patterns in Europe, Asia and the Americas, not much is known about the origins of craniofacial patterns exhibited by recent African populations. The Khoesan is an African population that has attracted the attention of physical anthropologists for more than a century. Despite being the focus of numerous craniometric analyses during this time, we still know little about their craniofacial evolution. Here I assess morphological variation in 153 individually dated Later Stone Age Khoesan crania (primarily Holocene) from South Africa's western, south-western, southern and south-eastern coasts and coastal forelands with the aim of reconstructing the evolution of craniofacial morphology in these recently extinct coastal Khoesan populations. I use information from the archaeological and skeletal records to identify events which may have been central to the development of recent patterns of craniofacial morphology in these populations. Hypotheses centre on three focus areas: (1) the origins of recognisably Khoesan cranial morphology; (2) the significance of late mid-Holocene fluctuations in Khoesan body size; and (3) the introduction of herding and population continuity/discontinuity at 2000 BP.

Coordinate data collected with a digitizer, are transformed into Euclidean distances between all landmarks. A subset of distances (48) is used to calculate Mahalanobis distances (D) between individual crania. Principle components analysis is used to investigate the primary form differences between crania. Coordinate data is also analysed via Generalised Procrustes Analysis to investigate size and allometric shape changes through time. Results indicate that Khoesan craniofacial morphology pre-dates the Holocene. Although there is a noticeable fluctuation in cranial size and concomitant changes in craniofacial shape during the late mid-Holocene, craniofacial form remains distinctly Khoesan-like. This study also demonstrates that despite minor increases in inter-individual morphological distances, there are no major changes in craniofacial form after 2000 BP. Results obtained in this thesis are consistent with long term continuity in Khoesan craniofacial morphology (at least 12 000 years) in the research region.

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CHAPTER ONE

INTRODUCTION

FOCUS OF THE THESIS

The biological evolution of the Khoesan of southern Africa remains poorly understood, in stark contrast to their much better known cultural record. This imbalance in knowledge is, however, not surprising. A sizable majority of prehistoric human remains from South Africa represent individual interments, making it difficult to extract biological information about the populations from which they derive. Additionally, this sample is geographically, temporally, and in certain cases genetically, diverse. However, the single most important impediment to research into origins of these peoples has been the lack of a large representative sample of dated remains. This dissertation reports on a craniometric analysis of a large sample (n = 153) of recently dated Later Stone Age (LSA) human crania from South Africa's western, south-western, southern and south-eastern coasts and coastal forelands. It explores morphological similarities and dissimilarities within this geographically and temporally diverse sample. In particular, it addresses the questions of how much variation existed and whether the cranial series represents a single population or derives from several distinct populations. It also identifies the major sources of variation. Ultimately, this research has a bearing on two issues: (1) the origins of recent patterns of Khoesan craniofacial morphology; and (2) the question of population continuity in the South African LSA, an issue that has proven difficult to address in archaeologically based studies.

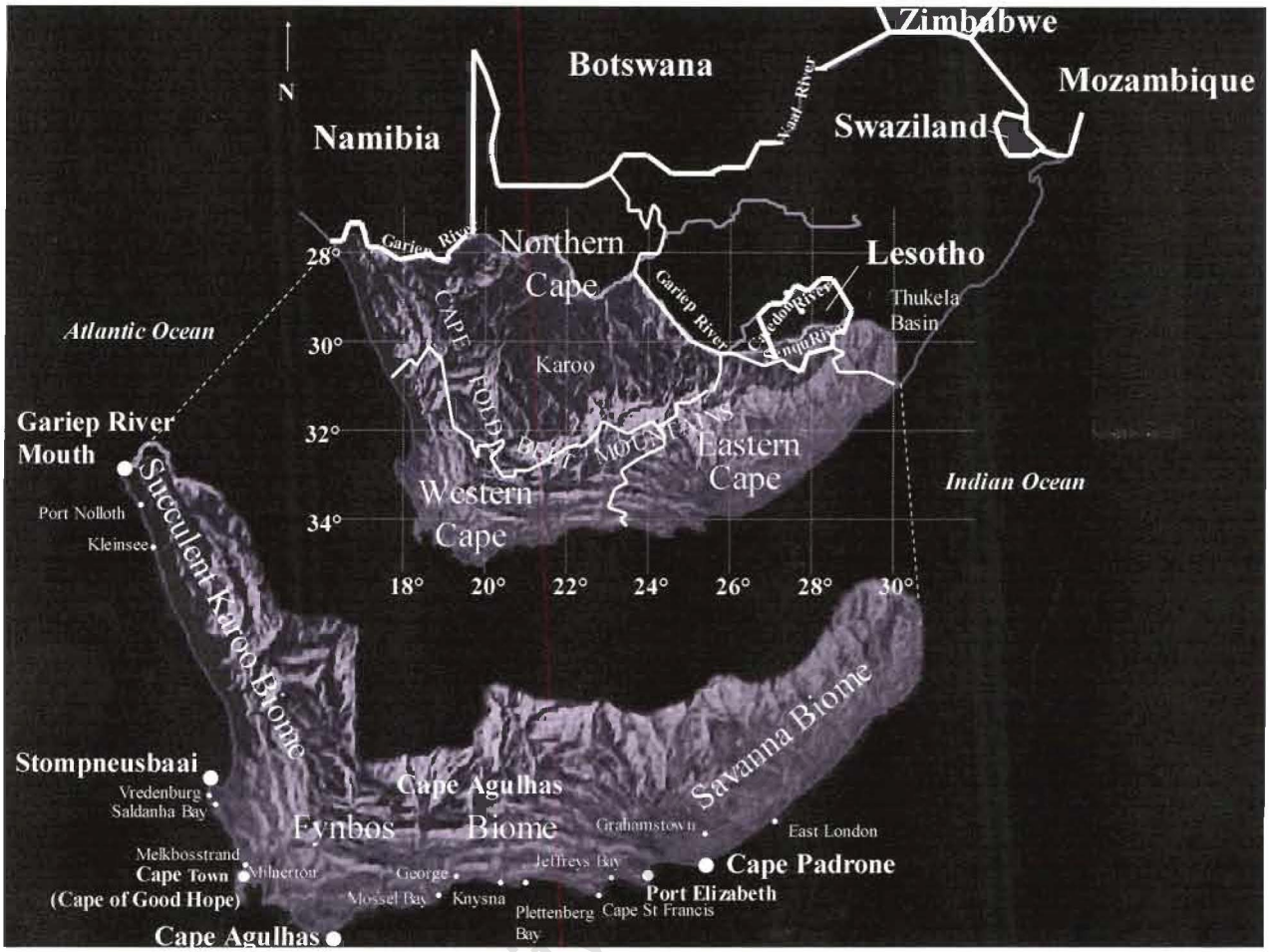

Figure 1.1: The location of the research region. This figure indicates the location of South Africa and surrounding countries, as well as the three provinces and ecological biomes located in the research region (raised section). Major towns and cities in the research region are also illustrated.

ENVIRONMENTAL AND ECOLOGICAL SETTING OF RESEARCH REGION

South Africa's western, south-western, southern and south-eastern coasts and adjacent coastal forelands (Figure 1.1) were the focus of continuous human occupation for much of the LSA. The LSA is the final phase in a tripartite division of the southern African Stone Age sequence which includes two earlier phases, the Earlier Stone Age (ESA) and Middle Stone Age (MSA) respectively (Goodwin and Van Riet Lowe 1929). Along with the Matopos Hills in Zimbabwe and the Thukela Basin in KwaZulu-Natal Province, these

coastal regions contain one of the richest LSA archaeological and palaeoenvironmental records in southern Africa. However, they stand alone in having the most complete LSA human skeletal record on the subcontinent. This record is extremely sparse for the terminal Pleistocene, but we have substantial numbers of skeletons or parts thereof from the Holocene, hence the focus of this thesis on the Holocene skeletal record. The existence of both a detailed human cultural record and a relatively abundant human skeletal record makes this coastline and adjacent coastal forelands ideal for investigating human biological and cultural change in South Africa during this period.

In terms of the current geo-political layout of South Africa, the research region spans three provinces, namely the Northern Cape, the Western Cape and the Eastern Cape Provinces (Figure 1.1). Following Heydorn and Flemming's (1985) and Heydorn's (1989) division of the South African coastline, the research region was sub-divided into four sub-regions in this thesis. These are the *western region* (from the mouth of the Gariep River to Stompneusbaai), the *south-western region* (from Stompneusbaai to Cape Agulhas), the *southern region* (from Cape Agulhas to Cape Padrone) and the *eastern region* (from Cape Padrone, eastwards). This sub-division was preferred because it characterises the climatic and oceanographic variability within the research region. The western region falls partly within the Western Cape Province and partly within the Northern Cape Province. Ecologically it is situated in the Succulent Karoo Biome. Unlike other coastal regions such as the south-western and southern regions, this region had experienced much lower levels of population density during the LSA. Situated to the west of the Karoo escarpment, the western region is primarily characterised by gently

undulating sandy plains interspersed with some hilly areas. Present-day vegetation is dominated by dwarf, succulent shrubs and grasses are generally rare. Climatically, the region is characterised by low winter rainfall, which varies between 20 and 290 mm per year, and extreme summer aridity (Rutherford and Westfall 1986; Low and Rebelo 1996).

The south-western and southern regions, in the Western Cape Province, preserve the most abundant LSA archaeological and human skeletal remains of any southern African regions. These two regions fall within the ecologically distinct Fynbos Biome (also known as the Cape Ecozone), an area marked by exceptionally high rates of biological diversity and endemism. The Fynbos Biome includes the Cape Fold Belt Mountains and coastal forelands. With a total surface covering 87 892 square kilometres (Cowling and Heijnes 2001), not only does this biome possess the highest density of plant species in the world, 70% or so of which are endemic (Goldblatt and Manning 2002), but it is also home to numerous endemic vertebrates (Branch 1988; Stattersfield *et al.* 1998; Brooks *et al.* 2001) and invertebrates (Picker and Samways 1996). Environmentally diverse, its mountains and valleys in particular, act as "population traps", providing fertile areas for species diversification (Kingdon 1989). Geographic isolation of many species is ensured by an extensive mountain range (Cape Fold Belt) backed up by an inhospitable semi-arid region, the Karoo, which collectively form an effective barrier between this region and the rest of Africa. Not only does this pose a formidable hurdle to the mobility of animals and plants between these coastal regions and the rest of Africa, but it probably also restricted contact between coastal human populations and those living in the South African interior during prehistory.

The south-western region consists of wide, primarily sandy coastal lowlands that lie between the Cape Fold Belt Mountains and the Atlantic Ocean. Today, it has a mediterranean-type climate with mild, wet winters and warm dry summers. The principal vegetation type is a mix of strandveld, renosterveld and coastal fynbos. Average rainfall ranges from less than 200 mm to 2000 mm per year. The southern region by contrast, is characteristically rocky. This region is situated on a coastal platform which is elevated to approximately 200 meters. Abutting the Cape Fold Belt Mountains in the north, this coastal platform has a maximum width of approximately 20 km in the west, and narrows to approximately 2 km in the east. The climate is warm and temperate with year round rainfall ranging between 200 and 1200 mm per year. Fynbos, typically taller species than that growing on the south-western region, also dominates. However, patches of afromontane forest occur in areas where rainfall is highest (Rutherford and Westfall 1986; J. Deacon and Lancaster 1988; Butchard 1995; Low and Rebelo 1996).

The eastern region falls within the Eastern Cape Province. Ecologically it is situated in the Savanna Biome. Geographically, it is situated south-east of the Karoo escarpment and east of the Cape Fold Belt. Present-day vegetation is primarily characterized by a grassy ground layer and a distinct upper layer of woody plants. Unlike grasses growing in the western, south-western and southern regions, the grasses in the eastern region are dominated by C 4-type grasses. Today, this region is predominantly summer rainfall, with rainfall varying between 235 and 1 000 mm per year (Rutherford and Westfall 1986; Low and Rebelo 1996).

THE LATE PREHISTORIC AND EARLY COLONIAL KHOESAN

The term "Koïsan" (now Khoesan) was a biological term coined by Leonhard Schultze in 1928, to refer to a large cluster of related indigenous southern African peoples, distinct from Negroids. Subsequently, Khoesan has also been used as a cultural and linguistic label (Barnard 1992). The first European contact with Khoesan peoples dates back to 1488, when the Portuguese mariner Bartolomeu Dias sailed his caravelle around the southern tip of Africa. Dias, and fellow Portuguese mariner Vasco Da Gama who followed Dias around the Cape of Good Hope in 1497, mentioned these peoples in their diaries. However, accounts were brief and not very informative. It was only after the Dutch East India Company (VOC) established the first permanent European settlement at Table Bay in 1652 that more informative accounts were produced on the culture and life ways of the Khoesan (Elphick 1985). Much was written about the Khoesan by these early settlers, however, the vast majority of accounts were fragmentary and often unreliable. The most voluminous was the 1652-1662 Journal of Jan van Riebeeck (Thom 1958), the first Dutch commander of the Cape, which commented extensively on the groups around the settlement and also occasionally on those living further inland. Nomadic herders and small groups of beachcombers who subsisted mainly by hunting-and-gathering, occupied much of the literature during the initial period of settlement, as these people lived close to the Dutch outpost. It was only later that contact was made with inland hunter-gatherer groups, when expeditions were despatched into the interior. The settlers adopted the name 'Strandlopers' for the beachcombers and 'Hottentots' for the herders. The herders referred to themselves as 'Khoekhoe' (previously Khoikhoi). The inland hunter-gatherers

were called Soaqua or Bushmen by the Dutch and 'Sonqua', 'Soaqua', 'Obiqua' or 'San' by the Khoekhoe (Barnard 1992; Boonzaier *et al.* 1996).

Early accounts widely declared that the nomadic pastoralists, beachcombers and inland hunter-gatherers represented mutually exclusive populations, each of whom possessed their own distinctive modes of social organisation, language and material culture. Expedition diaries in particular commented extensively on the hunter-gatherer bands in the interior. Typical descriptions of these hunter-gatherers included "poverty-stricken", "tiny people" and "plunderers and marauders" (Schapera and Farrington 1933; Thom 1958). In many instances these descriptions were juxtaposed against more favourable descriptions of the purportedly taller, better-off herders. As illustrated by these early accounts, the Dutch paid particular attention to perceived differences between the inland hunter-gatherers and herders. Differences in stature in particular were taken to signify ethnic differences between the practitioners of the two life ways. In this way, early perceptions contributed significantly to the establishment of a supposed dichotomy in ethnicity/life ways that became entrenched in South African Khoesan studies for much of its early existence.

While early colonists regarded inland hunter-gatherers and herders as genetically distinct populations, many early colonial accounts are rather ambiguous in their descriptions of how these indigenous groups were related to each other. Although inland hunter-gatherers and nomadic pastoralists are often portrayed as culturally and biologically separate entities, there also appear to have been many overlapping features of their socio-

economies (Thom 1958), bringing into question ideas about the mutual exclusivity of the two life ways. The original coastal groups encountered at first contact are now no longer in existence. From the outset of the colonial period, a process was set in motion whereby the Khoesan were systematically dispossessed of their land, stock and political power. Their biological and cultural demise was finally sealed by a devastating smallpox epidemic that swept through the Cape of Good Hope and surrounding regions in 1713. The integration of survivors into the social and economic structures of the colonial Cape, and the constant persecution of surviving bands living beyond the boundaries of the colony sealed their fate (Elphick 1977, 1985; Steyn 1990). As a result, apart from accounts by the early colonists, very little is known about the Cape's original coastal inhabitants. This situation is worsened by the fact that many of the early accounts about social and biological relationships amongst these indigenous folk remain unconfirmed. Did early colonial and prehistoric Khoekhoe pastoralists and San hunter-gatherers at the Cape represent related yet genetically discrete populations, or were they genetically indistinguishable? If they were genetically discrete populations, when and how did these differences come about?

EARLY KHOESAN ORIGINS

The issue of the biological origins of the Cape Khoesan runs deeper than just the problem of San and Khoekhoe origins. Phillipson (1982) hypothesised that the African Later Stone Age human fossil record represents three major human groupings: 1) a North African group related to modern Caucasoid populations; 2) an ancestral Negroid group in West Africa; and 3) an ancient Khoisanid, or Khoesan group that ranged over much of

southern, eastern and north-eastern Africa. Genetic research carried out over the last 20 to 30 years appears to reinforce the longstanding hypothesis that the Khoesan were the aboriginal population of southern, eastern and north-eastern Africa (Tobias 1978; Nurse *et al.* 1985). Serological research on recent Negro and San biological relationships emphasized the "exaggeratedly African" genetic character of the San, which was interpreted as evidence for their closer genetic affinity to ancestral African peoples (Tobias 1972, 1978). More recent genetic research continued in this vein. Soodyall and Jenkins (1992) placed the divergence between three major genetic groupings of sub-Saharan people - Khoesan, Pygmy and Negroid - at approximately 150 000 years ago. In addition to having an ancient genetic lineage, the Khoesan are positioned as genetic outliers in the context of sub-Saharan Africa in many genetic studies (Excoffier *et al.* 1987; Cavalli-Sforza *et al.* 1994; Watson *et al.* 1996; Chen *et al.* 2000). Interestingly though, there is a Y-chromosome genetic link between the Khoesan and some Ethiopian populations (Cruciani *et al.* 2002; Semino *et al.* 2002). Most genetic studies interpret this link as evidence for the ancestral position that the Khoesan occupy with regards to modern East Africans (*cf.* Cruciani *et al.* 2002; Semino *et al.* 2002). Another explanation may be that these populations shared a common ancestor in the past (Knight *et al.* 2003). Intriguing though the recent genetic evidence may appear, the existence of an ancient, once wide-ranging Khoesan population does not receive support from the osteological record (A. G. Morris 2002, 2003). After reviewing the fossil evidence for an extra-southern African presence (Galloway 1933; Leakey 1970; Tobias 1964, 1978), A. G. Morris (2002, 2003) was unable to find any unambiguous evidence for the presence of

Khoesan traits in several East African cranial specimens which in the past had been identified as Khoesan.

Claims that existing Khoesan populations represent the remnants of an ancient Pan-African population (Tobias 1972, 1978) have also not stood up to scrutiny of the South African fossil human record. On available evidence, it is not possible to assign unambiguously Late Pleistocene southern African fossil crania such as Klasies River and Border Cave to any contemporary African population (A. G. Morris 1992b; Wolpoff 1996). The undifferentiated morphologies displayed by the Klasies River and Border Cave specimens appear to be a feature of slightly later South African crania as well. The *ca.* 30 000 to 40 000 year old Hofmeyr cranium (ELM 24) is not distinctly Khoesan or Negroid (A. G. Morris and Grine 1999; A. G. Morris *et al.* 2005), while the Boskop calotte (PEM 120) differs significantly from both Negro and San populations (de Villiers and Fatti 1982).

A. G. Morris (2002, 2003) has argued that Khoesan cranial morphology arose relatively late in southern Africa. According to A. G. Morris' (2002, 2003) hypothesis, the ancestors of recent Khoesan populations underwent a bottleneck associated with the Last Glacial Maximum (LGM) at *ca.* 24 000 B. P. to 17 000 B. P. At this time the cool, dry glacial climate would have resulted in the aridification of much of southern Africa, particularly the inland regions. A scarcity of inland archaeological occurrences suggests significant depopulation of these areas (Mitchell 1990; Wadley 1993). At the same time, a large area of land would have been exposed along South Africa's southern coast, with

an extended coastal plain of over 100 kilometres at some places (van Andel 1989). Unlike the interior, the better watered southern coastal region displayed comparatively denser human occupation at this time (Parkington 1990). It is further hypothesised that the genetic isolation of this coastal population for the duration of the LGM would have resulted in genetic drift and directional selection. These evolutionary processes would eventually have lead to the differentiation of this population from other African populations and thus to the emergence of Khoesan populations (A. G. Morris 2002, 2003). At the end of the glacial period, there would have been a population expansion which would have resulted in the expansion of Khoesan morphology into the rest of southern Africa (A. G. Morris 2002).

Osteological evidence from primarily fragmented remains (Bräuer and Rösing 1989; A. G. Morris 1992 a, b) appears to support A. G. Morris' (2002) hypothesis of a relatively recent southern African origin of recognisably Khoesan cranial morphology. In accordance with his model, terminal Pleistocene/early Holocene human crania do indeed display a general Khoesan craniofacial pattern, particularly with regards to upper facial form (Bräuer and Rösing 1989). According to Bräuer and Rösing (1989), fossils such as the *ca.* 12 000 year old Fish Hoek cranium (Keith 1931; Schwartz and Tattersall 2003) and 10 000 year old Albany Man (Bräuer and Rösing 1989), possess the small, broad (euryprosopic) upper faces typical of recent Khoesan populations. These early specimens are said to differ from recent populations, however, in terms of neurocranial shape. While the long or dolichocephalic neurocranial shape appears to be dominant during the terminal Pleistocene/early Holocene, the medium headed or mesocephalic neurocranial

shape is said to be more common in recent populations. But the primary difference between terminal Pleistocene/early Holocene populations and recent populations relates to the larger size and greater robusticity of the early specimens (Bräuer and Rösing 1989).

THE DEVELOPMENT OF RECENT POPULATIONS

Although early 19th century archaeologists had noticed the variable nature of the South African LSA archaeological record (Goodwin and Van Riet Lowe 1929), the lack of dating methods prevented scientists from determining the true source of this variation. At the time, variation was widely interpreted as evidence of multiple migrations into the region during the course of the LSA. This idea was reinforced by the significant craniofacial variation evident in the LSA fossil record (Keith 1934; Meiring 1937). Recent archaeologists generally reject the view that the variation in the South African archaeological record is due to multiple migrations. Rather, the changes are interpreted in terms of *in situ* cultural developments amongst indigenous groups (H. J. Deacon 1976; J. Deacon 1984a, b). The only time that immigration is considered to have been a plausible cause of change is during the last 2000 years, when herding was introduced. Claims of population continuity in the South African LSA have, however, rarely been tested using biological data during the modern era. Where biological continuity/discontinuity has been investigated, results are questionable due to methodological problems (discussed in Chapter 3).

Recent archaeological research, rather than physical anthropology, has contributed most towards our understanding of the origins of recent prehistoric and early colonial coastal Khoesan populations. Over the last 30 years or so, archaeologists have made significant progress in elucidating South Africa's LSA archaeological record. Much of this research has been carried out along the country's western, south-western, southern and eastern coasts.

Archaeological evidence has confirmed the existence of two life ways (hunting and herding) in South Africa during the last 2000 years. There remains disagreement, however, about whether this equates with the existence of two economically and biologically distinct populations. One school proposes that hunter-gatherers and pastoralists formed two mutually exclusive socio-economic groups (A. B. Smith 1983, 1986, 1990, 1992; A. B. Smith *et al.* 1991; Yates and A. B. Smith 1993). The origin of Cape herders is attributed to the migration of genetically distinct pastoralist groups into the Cape at around 2000 years BP (P. Smith *et al.* 1992). The other school questions this rigid view and proposes that hunter-gatherers and herders represented segments of a culturally and biologically homogenous population. Within this population, people would have move back and forth between different economic strategies (Marks 1972; Schrire 1980, 1992; Elphick 1985; Schrire and J. Deacon 1989). Hunting-and-gathering is viewed as a "down" phase to which people who had lost stock would revert; once stock was re-acquired, they would revert back to herding, the "upward" phase (Elphick 1985). According to the adherents of this school, herding entered the region either by the acculturation of indigenous hunter-gatherer communities (Kinahan 1991), or via migrant

pastoralist groups who mixed genetically with local populations, eventually resulting in a genetically and culturally homogenous population (Elphick 1977, 1985).

Prior to 2000 BP, the archaeological record indicates that people exclusively practiced hunting-and–gathering. There is however evidence of two major shifts in technology and subsistence strategy within a hunting-and-gathering economy (H. J. Deacon 1976; J. Deacon 1984 a, b; H. J. Deacon and J. Deacon 1999; Mitchell 2002). The first occurred at *ca.* 12 000 BP, when the early LSA Robberg Industry, a predominantly microlithic industry, was replaced by the macrolithic Oakhurst Complex. At the same time, there was a broadly concurrent shift in food remains from large to small animals. The second shift occurred at *ca.* 8000 BP when there was a switch back to a microlithic stone tool industry, the Wilton Complex, but continued exploitation of small game animals. From 4000 BP, there was a marked increase in archaeological sites in many regions of South Africa suggesting an increase in overall human population size compared with early or mid-Holocene times. Subtle shifts in site organisation, food residue and cultural artefacts, suggest reduced mobility, increased sedentism and greater regional variation in material culture (Mazel 1989; Hall 1990; Binneman 1996; Jerardino 1996; H. J. Deacon and J. Deacon 1999). As in the case of the post-2000 BP period, the biological implications of these cultural and subsistence shifts are not known.

CONTEMPORARY KHOESAN POPULATIONS

According to Barnard (1992), Khoesan communities that have survived into the present share a number of distinctive cultural and biological traits. Although linguistically

diverse, all Khoesan groups speak click languages. Two major language divisions can be identified, namely "Bush"-speakers (Westphal 1963) and Khoe-speakers (Köhler 1962; Westphal 1971; Vossen 1984, 1988a, 1988b, 1990). Common features in territorial organisation, gender relations, kinship, ritual and cosmology are also shared across all Khoesan groups (Barnard 1992). Morphologically the Khoesan, as a population cluster, exhibit a number of characteristics such as light yellow-brown skin, epicanthic eyefolds, female steatopygia, female steatomerya, micronympha and the horizontal positioning of the non-erect penis in males which makes them markedly distinct from neighbouring Negroid groups.

Contemporary Khoesan populations such as the Kalahari San have for a long time occupied a central position in hunter-gatherer studies; most of what anthropologists know about the hunter-gatherer lifestyle has been influenced by studies of recent Khoisan populations. Historical and contemporary accounts focusing on the languages, belief systems and life ways of the San abound (W. H. I. Bleek 1875; W. H. I. Bleek and Lloyd 1911; G. B. Silberbauer 1961, 1963, 1972, 1973; Lee and DeVore 1968, Tanaka 1969, 1976, 1980; Wilmsen 1989; Wilmsen and Denbow 1990; Barnard 1992; Traill 1995). Similarly, skeletons of contemporary Khoesan populations have formed the basis of most early anthropological enquiry into Khoesan biological origins. Although these populations are the best available analogues for early Khoesan populations, they cannot replace studies of prehistoric skeletal material. For instance, prehistoric Khoesan communities along South Africa's coast occupied a resource-rich environment, while contemporary Khoesan groups have to a large extent been marginalised and isolated to the drier, less productive regions of southern Africa. Social and economic strategies

followed in marginal environments probably differ from those followed by prehistoric populations in more productive coastal environments, resulting in different biological adaptations. In addition, relatively recent events, including the operation of evolutionary forces, may mask or even obliterate patterns that were present in the past, which is especially problematic if one is trying to look at phenotypic relationships. It is well-known that some recent Khoesan populations show evidence of gene flow with Negroid populations (Cavalli-Sforza *et al.* 1994; Cruciani *et al.* 2002). Ideally, the population structure and evolutionary history of prehistoric and early colonial Cape Khoesan populations should be studied directly from their physical remains.

THIS STUDY

The cranium represents one of the most commonly studied parts of the human skeleton because it contains population-specific signatures (both now and in the past), and is also a functionally important part of the skeleton. It is accepted that craniofacial form (size + shape) is determined by the complex interplay between genetics (Relethford 1994, Sparks and Jantz 2002) and environment (Carlson 1976; Carlson and van Gerven 1977; Larsen 1981, 2002; van Vark *et al.* 2003). Within a population of interbreeding humans, members share a similar general cranial form that distinguishes them from non-members (Howells 1973, 1989; Relethford 1994). Biological changes in a population, be they genetic or due to environmental factors, are often reflected in changes in craniofacial morphological patterns. By systematically analysing craniofacial form in human populations over time and across space, one may be able to track the biological development of a population. Combining this morphological data with supporting

cultural and environmental data may allow one to identify genetic and/or environmental events that may have influenced biological change.

The last 10 000 years is recognised as the period during which recent Khoesan culture and social structure was established (J. Deacon 1984 a, b; H. J. Deacon and J. Deacon 1999). My research will contribute towards an understanding of the biological evolution of the coastal Khoesan during this period. An integrated approach is followed where cultural and ecological information is combined with craniometric information, all within a well-established temporal context. The LSA archaeological record provides information on subsistence, demographic and technological changes, thus informing on possible instances of gene flow into the region, while the ecological record provides information on environmental and climatic constraints. Hypotheses are constructed around this information, and craniometric data used to test them. These hypotheses which will be presented in Chapter 5, centre on three focus areas: (1) the origins of recognisably Khoesan cranial morphology; (2) the significance of late mid-Holocene fluctuations in Khoesan body size; and (3) the introduction of herding and population continuity/discontinuity at 2000 BP.

THESIS LAYOUT

The remainder of this thesis is composed of 7 chapters. The biological origin of recent human populations is the focus of many current projects around the world. It is the development of recent patterns of craniofacial variation, in particular, that has attracted the most attention. Chapter 2 reviews the evidence for the origins of recent patterns of

craniofacial morphology in human populations from other regions of the globe. Chapter 3 provides a history of the assessment of craniofacial diversity in South African Khoesan populations. This chapter looks at how the study of craniofacial variation in the Khoesan has changed over the past century, and also at how changes in approaches have altered conclusions. Chapter 4 reviews our current knowledge of the South African human fossil record for the MSA and LSA. Chapter 5 provides an in depth overview of the climate, environment and regional archaeology of the Cape coastal regions and greater South Africa during the terminal late Pleistocene and the Holocene. This information is used to identify demographic changes and possible population migrations. Hypotheses to be tested are also presented at the end of this chapter. Chapter 6 describes the materials and methods employed in this study. Results of the analyses are presented in Chapter 7. The implications of these results are discussed and concluding remarks offered in Chapter 8.

CHAPTER TWO

HUMAN CRANIOFACIAL MORPHOLOGY DURING THE TERMINAL PLEISTOCENE AND HOLOCENE

INTRODUCTION

The related questions of when and how recent patterns of human craniofacial morphology emerged have been the focus of much physical anthropological research in recent decades (see references below). A great deal of evidence accumulated during this time, suggest that it was only during the Holocene that many of the craniofacial traits that characterise contemporary geographic populations and sub-populations were established. In this chapter I review the key issues relating to the emergence of recent patterns of human craniofacial morphology around the world.

RECENT PATTERNS OF HUMAN CRANIOFACIAL VARIATION

Genetic and craniofacial studies have highlighted the relative biological homogeneity of recent human populations. Compared to our nearest primate relative, the chimpanzee, recent humans display much lower levels of genetic differentiation between geographically separated populations (Fischer *et al.* 2004). This finding is supported by other researchers as well (Van Vark 1994; Cavalli-Sforza and Cavalli-Sforza 1995). Analyses of the worldwide variation in allele frequencies for a number of genetic markers (Lewontin 1972; Latter 1980; Ryman *et al.* 1983) and DNA polymorphisms (Barbujani *et al.* 1997; Jorde *et al.* 2000) found that genetic variation among major geographic groupings of humans account for only between 6% and 10% of total genetic variation,

while genetic variation among local populations within geographic regions account for between 5% and 8% of total variation. These figures compare well with phenotypic data (as measured by craniometric traits) which indicate that 11-14% of human cranial variation occurs between regions (Relethford 1994, 2002). In other words, the vast bulk of genetic and morphological variation is shared across modern human populations; very little distinguishes them from each other.

Despite humans being relatively homogenous in terms of genotype and phenotype, some important geographic differences in craniofacial morphology do exist. Research carried out by Howells (1973, 1989, 1995) elucidated these differences, and showed that it is fairly easy to determine the ancestry of a person based on their craniofacial morphology. According to Howells (1989), Europeans have relatively broad skulls, with low vaults. Faces are retracted and small, but nasal regions are projecting. Sub-Saharan Africans have convex foreheads and minimal supra-orbital development. Upper nasal regions are very flat and wide, while faces are broad across the nose and eyes. Faces are relatively short and lower facial regions are not very projecting. Within sub-Saharan Africans, the Khoesan generally have smaller crania than other populations, but still display a general African pattern, namely low faces and flat, broad noses. Frontal and occipital bones are convex. Egyptians, like other North Africans, resemble Europeans rather than sub-Saharan Africans in that they too have retracted faces and prominent upper noses. Upper faces, noses and palates are generally quite narrow. Australo-Melanesians display marked supra-orbital development and strong frontal regions. Upper noses and inter-orbital spaces are narrow and lower faces are projecting. In these aspects they differ from sub-

Saharan Africans. Similar to sub-Saharan Africans, though, Australo-Melanesians have short, broad upper faces. East Asians have high vaults and faces. Upper-facial regions are flat and sub-nasal and lower facial regions retracted. Native American populations share many cranial features with East Asians. These features include relatively broad sphenoid and palatal breadths, and high faces. On the other hand, vaults are low and broad at the base. In profile, frontals are flat and parietals long. As in East Asians, faces appear relatively flat, but sub-nasal regions are less so. Unlike East Asians, upper nasal regions are prominent (Howells 1973, 1989).

These regionally distinct craniofacial patterns may have developed relatively recently (Sarich 1997). During the Pleistocene and very early Holocene, human populations in many regions of the world apparently displayed much higher levels of within-population and within-region craniofacial diversity than is the case in recent populations (Van Vark 1990; Van Vark *et al.* 1992; Cunningham and Wescott 2002). Although it has to be remembered that sample sizes for these early populations are small, it does appear that the variation present in these populations fell outside of the limits of variation displayed by contemporary human populations.

HUMAN CRANIOFACIAL VARIATION IN THE PLEISTOCENE/VERY EARLY HOLOCENE

Compared to modern levels of intra-population craniofacial variation, the Late Pleistocene Zhoukoudian Upper Cave 101, 102 and 103 fossil crania demonstrate extreme levels of within-population diversity (P. Brown 1999; Cunningham and Wescott

2002). Weidenreich (1939) characterised Upper Cave 101 as "Mongoloid", Upper Cave 102 as "Melanesoid" and Upper Cave 103 as "Eskimoid". More recent analyses have found that Upper Cave 101 clustered closest to recent Polynesians, while Upper Cave 103 clustered with recent Australo-Melanesians (Cunningham and Jantz 2003). When these three crania are compared using Mahalanobis distances (Mahalanobis 1936; Van Vark and Schaafsma 1992), all three exhibit inter-individual distances that are in excess of distances expected for individuals belonging to the same population (using criteria applied to modern populations), despite the sample being spatially and temporally restricted (Cunningham and Wescott 2002). High levels of diversity also appear to have been present within geographic regions. When Van Vark *et al.* (2003) used Mahalanobis' D^2 distances to compare 35 European Upper Palaeolithic crania to a geographically diverse sample of recent human crania, five resembled recent Pacific Islanders, ten resembled recent Australian Aborigines, four resembled recent Africans and sixteen resembled recent Europeans. J. F. Powell and Neves (1999) demonstrated that Paleo-Indian populations from the terminal Pleistocene/very early Holocene are similarly diverse. Using typicality probability to determine which modern populations Paleo-Indian crania resembled, these researchers found that two resembled recent Africans, one resembled recent Europeans, three resembled recent Australasians, one resembled recent Polynesians and only one resembled recent Native Americans (Powell and Neves 1999).

Not only do human populations from the Pleistocene/early Holocene display exceptionally high levels of intra-population diversity, but they also rarely resemble their supposed contemporary descendents within the various geographic regions, as illustrated

above. Prior to a recent increase in the analysis of terminal Pleistocene/early Holocene American crania, most archaeological, genetic and linguistic evidence pointed towards a single terminal Pleistocene migration of ancestral Native American populations from East Asia via Beringia to the Americas (Nichols 1990; Bonatto and Salzano 1997; Nemecek 2000; Thomas 2000). Here, these Paleo-Indian populations were thought to have developed into modern Native Americans through a process of *in situ* evolution. Since Paleo-Indians were widely regarded as the ancestors of recent Native American populations, anthropologists widely believed that these early populations would display a strong resemblance to recent populations in terms of craniofacial morphology. However, recent studies investigating the origins of Native Americans using cranial material have highlighted a distinct discontinuity in the craniofacial morphologies of terminal Pleistocene/early Holocene Paleo-Indian populations and recent Native American populations. In analyses of South American human craniofacial variation during the Holocene, Munford *et al.* (1995) and Neves *et al.* (1996, 1999a) have determined that craniofacial morphology changed from crania characterised by long, narrow neurocrania and low, narrow, projecting faces, to crania characterised by short, wide neurocrania and high, wide, retracted faces. Similar morphological changes were observed in North American populations (Powell and Neves 1999; Jantz and Owsley 2001). In addition, Paleo-Indians display a morphological resemblance to recent Australian Aborigines and Pacific Islanders, rather than to recent Native Americans or East Asians (Neves and Pucciarelli 1998; Neves *et al.* 1999a, b; Owsley and Jantz 1999; Powell and Neves 1999; Jantz and Owsley 2001; González-José *et al.* 2003, 2005; Neves *et al.* 2003). This lack of morphological continuity between early and late Native American populations is

surprising in the context of the long-held theory that recent Native Americans are the descendents a single migration of Paleoamericans from East Asia.

Many other regions around the world display a similar pattern of discontinuity in craniofacial form between terminal Pleistocene/very early Holocene and recent populations (Henneberg 1988). Late Pleistocene Chinese specimens such as Zhoukoudian Upper Cave specimen 101 and Liujiang (Weidenreich 1939; Kaminga and R. V. S. Wright 1988; Van Vark and Dijkema 1988; Howells 1989, 1995; Cornell 1998) and Malaysian specimens such as Gua Gunung (Matsumura and Zuraina 1999) do not resemble modern Asians. Similarly, European Upper Paleolithic populations differ from modern Europeans (Frayer 1980, 1984; Van Vark and *et al.* 2003). Instead, these early Europeans tend to resemble recent populations like Australian Aborigines and Africans in craniofacial morphology (Stringer and McKie 1996; Van Vark *et al.* 2003). In general, Pleistocene/very early Holocene human craniofacial morphology, particularly in Europe and Asia, is quite robust; faces are low, narrow, and projecting; neurocranial shape is often dolichocephalic or long-headed. It is only from the mid-Holocene onwards that craniofacial morphology starts to resemble that of modern populations within these regions. At this time crania are small and gracile; faces are shorter, broader and retracted; neurocrania are shorter and wider (brachycephalic) (Carlson and Van Gerven 1977; Howells 1983; Spoor *et al.* 1999; Van Vark *et al.* 2003).

Not all regions of the globe display this discontinuity in craniofacial form between early and modern populations. Peripheral populations such as Australian Aborigines, Fuegians

and Patagonians tend to resemble the morphologies of pre-Holocene populations, especially in overall cranial size and robustness. Although, there are slight reductions in Australian Aborigine craniofacial dimensions during the Holocene, Aborigines remain one of the most robust recent human populations (Lahr and R. V. S. Wright 1996). Recently extinct populations such as the Fuegians and Patagonians from South America are also extremely robust in comparison to recent human populations from Europe, Asia and other parts of the Americas (Lahr 1995; Lahr and Wright 1996).

EXPLAINING THE DISCONTINUITY IN CRANIOFACIAL FORM

As illustrated above, there is mounting evidence that the patterns of craniofacial variation that characterise modern human populations developed relatively recently. Nevertheless, there is widespread disagreement amongst anthropologists regarding the probable mechanisms involved in the emergence of recent craniofacial patterns. It is often the case that researchers study the same prehistoric population but propose totally different explanations for change in craniofacial form. For instance, Morant (1925) and C. G. Turner and Markowitz (1990) suggested that population migration may explain differences in the cranial morphologies of Mesolithic and Neolithic Nubian populations. LeBlanc and Black (1974) and Carlson and Van Gerven (1977) however argued that these craniofacial changes were not due to any outside genetic influences, but were instead the result of reduced stress on the masticatory apparatus as a result of the spread of cooking technology during the Neolithic. Similarly, as noted above, it has long been suggested that Native Americans developed *in situ* from a single migration of East Asians during the terminal Pleistocene (Swedlund and Anderson 2003; Van Vark *et al.* 2003).

There now appears to be an emerging view amongst many physical anthropologists studying Native American origins that there were instead several human migrations into the Americas during the Late Pleistocene and Holocene, not all necessarily originating in East Asia (J. F. Powell and Neves 1999; Jantz and Owsley 2003; Neves *et al.* 2003).

FACTORS THAT INFLUENCE CRANIOFACIAL MORPHOLOGY

It is now well established that cranial morphology is determined by the complex interplay of environmental and genetic factors (Lahr and Wright 1996; Wood and Lieberman 2001; González-Jozé *et al.* 2004). What is less certain however is the relative influence of genetic versus environmental factors on cranial morphology. Disagreements amongst physical anthropologists regarding this issue underlie much of the uncertainty surrounding the emergence of recent patterns of craniofacial variation. Some researchers argue that since the human cranium is relatively plastic, its form is strongly influenced by the external environment. For this reason, it cannot reliably be used as a surrogate for genes, and is consequently unsuitable for investigating ancestral-descendent relationships between recent and prehistoric populations (Goodman 1995; Goodman and Armelagos 1996; Armelagos and Van Gerven 2003; Swedlund and Anderson 2003; Van Vark *et al.* 2003). These researchers normally attribute the changes evident in the craniofacial morphologies of many human populations at the end of the terminal Pleistocene/Early Holocene to biomechanical changes associated with the advent of agriculture (Larsen 1981; Ruff 1987, 1999, 2000). On the other hand, there are those who have argued that despite being characterised by a certain degree of plasticity, cranial morphology is primarily influenced by genetics. This school believes that the unique craniofacial

morphologies displayed by human populations around the world contain population specific signatures that developed primarily as a result of alterations in the genotype. Since overall craniofacial form is primarily influenced by changes in the genotype, this school argues that ancestral-descendent relationships can be investigated by an analysis of craniofacial form, and that such an analysis can inform on past patterns of population structure and history. Although natural selection has been implicated as a factor in the origins of recent patterns of craniofacial variation (Whitlock 1999; Roseman 2004), the primary causes, as considered by these researchers, are neutral evolutionary forces such as mutation, migration (gene flow) and genetic drift (Relethford 1994, 2002; Relethford and Harpending 1994; González-Jozé *et al.* 2005).

PHENOTYPIC PLASTICITY

American anthropologist, Franz Boas (1912a, b) demonstrated relatively early on that the human cranium is characterised by a degree of plasticity, and that cranial form may be influenced by the environment. After the collection and analysis of cranial measurements from over 13 000 subjects, Boas was able to demonstrate that slight differences in cranial form existed between immigrant Americans and their American born offspring. This finding allowed him to proclaim that environment and not genetics was the primary determinant of cranial form. The central theme of his study was that the cranium was plastic and responds to environmental forces during growth and development. He argued that since the cranium was shaped primarily by environmental forces, it could not be used as a reliable representation of biological differences between people.

Since Boas' (1912a, b) revelation almost a century ago, it has become increasingly evident that genes may give rise to a range of phenotypes depending on environmental conditions (Gilbert 2001; Pigliucci 2001; Bateson *et al.* 2004; West-Eberhard 2003, 2005). Particular environmental factors which are thought to have been responsible for the establishment of recent craniofacial morphologies are reductions in biomechanical stress associated with the advent of food processing (Hylander 1972, 1977; LeBlanc and Black 1974; Carlson and Van Gerven 1977; Hylander and Johnson 1992; Spencer and Demes 1993; Bouvier and Hylander 1996; Lieberman 1996; Hernández *et al.* 1997; Giesen *et al.* 2003; Lieberman *et al.* 2004; Sardi *et al.* 2004) and dietary shortages associated with increased sedentism and population growth (Sofaer *et al.* 1971; Sofaer 1973; Macchiarelli and Bondioli 1986).

The switch to agriculture in many regions around the world appears to be correlated with a *relaxation of stress* on the skeleton. Larsen (1981) reports a correlation between the reduction in size in the post-cranial skeletons of prehistoric Georgians and a switch to a mixed hunter-gatherer/corn agriculture economy. Ruff (1987, 1999, 2000) has reported similar evidence for a reduction in post-cranial robusticity in populations that shifted to agriculture and a sedentary lifestyle in other regions of the Americas. A relaxation of stress on the skeleton appears to have affected not only the post-cranial skeleton, but also the cranium. The shift to agriculture generally saw a greater emphasis being placed on softer carbohydrate staples and cooked foods, which in turn may have translated into a relaxation of masticatory strain on the craniofacial skeleton, and a corresponding reduction in cranial size and robusticity. Experimental work has demonstrated that strain

(e.g. chewing of tough foodstuff) placed on the skeleton of maturing animals can stimulate periosteal growth and inhibit resorption of bone (Lieberman 1996; Lieberman *et al.* 2004). This in turn can lead to greater skeletal robusticity (Lieberman 1996). This process also appears to affect the craniofacial morphology of recent human populations (Lieberman 1997). For instance, the Inuit often eat frozen flesh, or use their dentition as tools. Inuit crania in turn display robust muscle attachment areas, mandibular and palatal tori, sagittal keeling and robust mandibles. Hylander (1972, 1977) has argued that many of these craniofacial features, particularly those related to the masticatory apparatus, may be attributed to the affects of biomechanical strain on the Inuit cranium. Hernández *et al.* (1997) have hypothesised that some of the craniofacial features displayed by the Fuegians may in part be due to biomechanical stress. These include wide bizygomatic breadths, wide biauricular breadths, wide bifrontal breadths and cheek heights (Hernández *et al.* 1997). A reduction in masticatory stress may in turn lead to significantly less bone growth in the craniofacial skeleton (Lieberman 1996; Lieberman *et al.* 2004). Carlson and Van Gerven (1977) have argued that craniofacial changes in prehistoric Sudanese Nubians who had undergone changes in subsistence strategy may have been due to a relaxation of stress on the cranial skeleton. Prior to subsistence changes, the general skull shape of this population was long and narrow, but with a change in diet, became relatively shorter and rounder (Carlson and Van Gerven 1977). Similar patterns have also been observed in other human populations around the world that underwent dietary changes (Brace and Mahler 1971; Calcagno and Gibson 1988; Lucaks 1984). In North America, where agriculture spread relatively late (Matson 1999; B. D Smith 1995), there

were significant reductions in skeletal robusticity levels after the introduction of agriculture (Ruff *et al.* 1994; Ruff 2000; Ruff and Larsen 2001).

Arguments in favour of biomechanical factors being the main cause of change in craniofacial morphology during the terminal Pleistocene/early Holocene have been criticised by others (Macchiarelli and Bondioli 1986; Jantz and Owsley 2003). The reasons for this criticism are two-fold. Firstly, some populations such as Australian aborigines display an overall reduction in cranial size in the absence of major dietary changes (P. Brown 1987, 1989, 1992). Secondly, experimental studies on non-human primates and other animals show that masticatory strain does not affect all regions of the cranium equally (Fields 1991; Hylander and Johnson 1992; Spencer and Demes 1993; Bouvier and Hylander 1996).

The cranium is not a single structure, but consists of two distinct regions, the viscerocranium and neurocranium, which perform separate functions and have different developmental histories (Cheverud 1982). The viscerocranium is the region of the cranium used during feeding and breathing. Parts of it, particularly those associated with the processing of food (palate and maxillary region), are subjected to muscular loading throughout life (Cheverud 1982). Hence, the affects of masticatory strain appear to be primarily *localised in the lower face* (Fields 1991; Hylander and Johnson 1992; Spencer and Demes 1993; Bouvier and Hylander 1996). The neurocranium, on the other hand, encloses the brain. Although muscles related to mastication are attached to it (e.g. temporalis), the neurocranium displays low levels of masticatory strain in comparison to

the lower face (Hylander and Johnson 1992; Spencer and Demes 1993; Bouvier and Hylander 1996). Its form appears to be primarily determined during growth by the expanding brain (Wood and Lieberman 2001), while biomechanical and environmental influences (Lahr 1996) probably play a lesser role.

Wood and Lieberman (2001) determined that the palate and maxillary regions of extant *Homo*, *Pan*, *Gorilla*, *Pongo* and *Colobus* display high levels of intra-specific variation, while the cranial base, neurocranium and upper facial regions display low levels. They conclude that the variability displayed by the palate and maxillary regions of primates may be explained by the high levels of biomechanical strain acting on these regions in comparison to reduced levels acting on the neurocranium, basicranium and upper-facial regions. A recent comparison of the cranial morphology of 18 hunter-gatherer and farming communities from South America also confirm the plasticity of the maxillary components compared to the relative stability of the upper face, neurocranium and basicranium. González-José *et al.* (2005) found that farmers and hunter-gatherers could not be distinguished from one another on the basis of total cranial form. However, there was greater separation between groups practicing the two subsistence strategies when only maxillary components were compared. Importantly though, González-José *et al.* (2005) note that the levels of differentiation amongst subsistence strategies never surpassed the level of inter-population differentiation, thus pointing towards a strong genetic influence on overall craniofacial form.

Macchiarelli and Bondioli (1986) have suggested that food shortage and an increase in disease load, results of an increase in population size and greater sedentism during the Holocene, may well have played a role in the observed changes in craniofacial morphology (Macchiarelli and Bondioli 1986). Although Macchiarelli and Bondioli's (1986) argument was largely based on sedentary agricultural communities, it also has relevance for hunter-gatherers undergoing intensification without the emergence of agriculture. Studies on prehistoric hunter-gatherer communities have predicted that populations living just prior to a major cultural transformation should display a decline in health and a *decrease in stature* due to nutritional problems and social disruption brought on by food shortages (Cohen and Armelagos 1984; P. L. Walker and Lambert 1989). According to Larsen (2002), cells that are responsible for the development of dental and skeletal tissue are easily disrupted by negative environmental influences when the tissue is being formed. Children are thus most at risk. Under circumstances of socio-economic stress, food shortages and unhealthy living conditions may inhibit long bone growth in children, preventing them from reaching their growth potential (Ruff 2002). Steckel *et al.* (2002) note that various forms of biological stress will depress and even halt growth rates under severe circumstances. In addition, under sustained biological stress, depression of growth rates may lead to permanent stunting (Steckel *et al.* 2002). It is not only the postcranial skeleton that may be affected by food shortage, unhealthy living conditions and increased stress. Studies on non-human primates (Pucciarelli *et al.* 1990, 2000; Pucciarelli and Dressino 1996; Dressino and Pucciarelli 1997, 1999; Cónsole *et al.* 2001) and rats (Pucciarelli 1980; Engstrom *et al.* 1982; Pucciarelli and Goya 1983; Pucciarelli *et al.* 1984; J. P. Miller and German 1999; Cesani *et al.* 2003) demonstrate that dietary

constraints *delay* growth in cranial size, which in turn *alters* cranial form. Teeth may equally display a reduction in size and robusticity under conditions of dietary constraints (Sofaer *et al.* 1971; Sofaer 1973; Macchiarelli and Bondioli 1986).

Like biomechanical stress, changes in craniofacial morphology resulting from dietary constraints also appear to affect certain regions of the cranium more than others. The region that is most affected by dietary constraints is also that with the greatest growth rate, namely the viscerocranium. On the other hand, the neurocranium which grows more slowly and for a longer period is less affected (Dressino and Pucciarelli 1997, 1999; Miller and German 1999). Biomechanical stress and dietary shortages are unlikely explanations for the changes we see in human craniofacial morphology during the terminal Pleistocene/early Holocene as many populations display comprehensive changes which affect the viscerocranium as well as the neurocranium and basicranium. Instead, a large part of the cranial changes are better explained by changes in the genotype of many geographic populations at the time.

GENETICS

Boas (1912a, b) is credited with originally demonstrating the relatively plastic nature of the human cranium and the role that environmental factors play in altering craniofacial form, however, he never claimed that cranial plasticity was unlimited, or that there was no genetic component involved in the determination of cranial form (Gravlee *et al.* 2003). On the contrary, Boas (1912a) noted that the fact that there was no convergence in cranial morphology between Europeans and indigenous populations in the Americas and the East

Indies proves that the plasticity of the cranium was not the only determinant of cranial form, but that genetics plays an important role.

Devor (1987), who calculated the heritability of craniometric traits in four human populations, reported that heritability ranged from 0.48 to 0.61 across all four populations, with an average heritability of 0.55. He argues that this is a conservative estimate, since many of the measurements were performed on soft tissue which would have been more sensitive to environmental factors than bone. Using Devor's (1987) estimate of the average heritability of craniometric traits and Howells' (1973, 1989) worldwide data set on human craniometric measurements, Relethford (1994, 2002) determined that there was a significant correlation between phenotypic distance (as measured by craniometric traits) and genotypic distance (as measured by genetic markers and mitochondrial DNA) among major recent human population groupings around the world (Relethford 1994, 2002; Relethford and Harpending 1994; González-Jozé *et al.* 2004; Roseman 2004). The relationship between genotype and phenotype has been modelled as $G=h^2\mathbf{P}$, where h^2 is an estimate of the average heritability for craniofacial traits and **P** is the phenotypic variance-covariance matrix (Cheverud 1988; Williams-Blangero and Blangero 1989).

Levels of heritability are not equally distributed across the cranium though. As pointed out above, the neurocranium and basicranium are less likely to be affected by environmental factors than parts of the viscerocranium (in particular the maxilla and palate), and are thus better sources of phylogenetic and taxonomic information (Fields 1991; Miller and German 1999; Lieberman 2000; Wood and Lieberman 2001; González-

Jozé *et al.* 2005). This is because the basicranium and neurocranium are functionally and developmentally different to the viscerocranium. Lieberman *et al.* (2000) note that the basicranium, unlike the neurocranium and viscerocranium which develop intramembranously from neural crest-derived tissue, develops instead from endochondral ossification processes in which mesodermally-derived cartilaginous precursors develop *in utero* and are gradually replaced by bone after birth. It also matures early (Moore and Lavelle 1974) and is consequently relatively unaffected by environmental factors during development. Although the neurocranium takes relatively longer to reach maturity and is developmentally different to the basicranium, its form is primarily determined by the growing brain, as mentioned above (Wood and Lieberman 2001). Environmental factors probably play less of a role on the form of the neurocranium because external restrictions on neurocranial form would place too much strain on a full-size brain (Miller and German 1999). Since environmental factors play a relatively minor role in the morphology of the basicranium and neurocranium, significant changes in these regions are likely to be due to genetic factors.

When viewed from a world-wide perspective, most of the craniofacial variation displayed by contemporary human populations is not consistent with the affects of environmental factors (Relethford 2002, 2004). This is the case despite the known influence of environmental factors on the viscerocranium (Lahr and Wright 1996; González-Jozé *et al.* 2005). On the contrary, craniofacial variation displays a distinct regional patterning which is consistent with genetic differences between populations (Relethford 2002, 2004). Genetic data shows that contemporary human populations which are separated by

great geographic distances are genetically more divergent than populations that are separated by smaller distances (Bowcock *et al.* 1991; Cavalli-Sforza *et al.* 1994; Relethford and Harpending 1995). Similarly, Howells (1989), using Mahalanobis' D^2 distances to investigate phenotypic distances between the crania of 28 human populations from around the world, found that in terms of craniometric distances, human populations also clustered broadly according to their geographic origins.

THE ORIGINS OF RECENT PATTERNS OF CRANIOFACIAL VARIATION

A majority of the geographic structuring of craniofacial traits across geographic space is consistent with genetic changes under the influence of *neutral evolutionary forces* such as mutation, migration (gene flow) and genetic drift (Relethford 2002, 2004; Roseman 2004; González-Jozé *et al.* 2005). The dispersed nature of human populations appears to have been an important factor in the establishment of this structuring of craniofacial traits. As mentioned above, there is a positive relationship between increasing geographic separation on the one hand, and phenotypic and genetic distance among recent human populations on the other. Relethford (2002) notes that this structure is consistent with the isolation-by-distance-model (S. Wright 1943; Relethford *et al.* 1981; Konigsberg 1990). The isolation-by-distance-model predicts that in the absence of natural selection and under neutral expectations, genetic similarity between populations will decrease exponentially as the geographic distance between them increases because of the limiting effect of geographic distance on rates of gene flow (Relethford 2002). Genetic and phenotypic distances between populations would thus be bigger at greater geographic

distances than at shorter geographic distances (Relethford *et al.* 1981; Harpending and Ward 1982; Williams-Blangero and Blangero 1989; Konigsberg 1990; Relethford 2002).

According to Relethford (2001a), neutral evolutionary forces have the potential to structure intra-and inter-population biological diversity in a variety of ways. The structure depends on the particular balance that exists between mutation, gene flow and genetic drift at any particular time. All things being equal, mutation and gene flow will initially *increase* genetic and phenotypic diversity within a population, but in time, genetic drift will *decrease diversity*. Eventually, a population will reach *equilibrium*, whereby an increase in diversity due to mutation and gene flow will be countered by an equivalent decrease in diversity due to genetic drift. Changes in any of these three forces may lead to significant alterations in intra- and inter-population diversity. For example, an increase in gene flow (e.g. through increased migration between populations) would not only lead to a significant increase in intra-population genetic and phenotypic variation, but will also have a homogenisation effect across populations. On the other hand, an increase in genetic drift (e.g. through a decrease in population size) would not only lead to a significant reduction in intra-population genetic and phenotypic diversity but also to an increase in inter-population diversity (Relethford 2001a).

As previously mentioned, pre-Holocene human populations in many regions of the world are characterised by levels of intra-regional and intra-population cranial variation that exceed levels seen in contemporary populations. The high levels of heterogeneity which appears to have characterised these early human populations could be explained by the

combined effects of unfavourable Late Pleistocene climatic conditions (Sarich 1997) and generally small population sizes (Sokal and Uytterschaut 1987; Barbujan *et al.* 1995). Unlike the relatively stable and generally climatically mild Holocene, much of the Late Pleistocene was characterised by extreme fluctuations in climate which included glacial and inter-glacial periods (Childe 1951; Bar-Yosef and Meadow 1995; P. U. Clark *et al.* 1999). Sarich (1997) and Lahr and Foley (1998) have argued that the various cold spells which characterised the Late Pleistocene promoted aridity and growth of the ice caps, conditions which played a paramount role in the fragmentation of already small human populations. The isolation of human populations in turn led to a reduction in gene flow between populations and instead promoted genetic drift, leading to the extinction of some genetic lineages and an increase in craniofacial variation between populations.

The actions of genetic drift may explain an apparent mismatch that exists between the genetic and morphological data for contemporary populations. Despite apparent discontinuities in craniofacial morphology, contemporary Europeans, Asians, and Americans can trace their genetic origins back to the Late Pleistocene (Nichols 1990; Cavalli-Sforza *et al.* 1994; Cavalli-Sforza 1997; Harpending *et al.* 1998; Semino *et al.* 2000; Gibbons 2000; Van Vark *et al.* 2003). This led to some questioning the reliability of using craniofacial morphology to investigate ancestral-descendent relationships between recent and early populations (Swedlund and Anderson 2003; Van Vark *et al.* 2003). Jantz and Owsley (2003) however, note that contemporary human lineages may represent only a small percentage of the lineages that once existed. The recent analysis of ancient mtDNA from two Late Pleistocene-aged anatomically modern human fossils,

namely Lake Mungo 3 (Adcock *et al.* 2001; Relethford 2001b) from Australia and Villabruna (Di Benedetto *et al.* 2000) from Europe, indicates that these specimens possess mtDNA lineages that are not found in modern Australians and Europeans respectively. Although there is no way of estimating how many anatomically modern human lineages became extinct, it is interesting to note that despite the paucity of ancient DNA data, two extinct anatomically modern human lineages have already been identified. Jantz and Owsley (2003) argue that it is possible that the human fossil record represents many extinct anatomically modern human lineages. When we compare the crania of recent and Pleistocene humans, the chances of comparing an extant to an extinct lineage are relatively high. However, when we study the DNA of recent populations, analyses are being carried out on lineages that have survived up to the present. By design, we are only capable of studying lineages that are continuous between the Pleistocene and Holocene. This would lead to a false impression of a mismatch between the cranial and genetic data (Jantz and Owsley 2003).

Sarich (1997) notes that the greater homogenisation of craniofacial morphology evident in Holocene populations may be explained by an amelioration of climatic conditions after the Last Glacial Maximum (LGM) about 15 000 years ago and the onset of a stable Holocene climate. At this time, temperate conditions facilitated renewed gene flow between populations and regions. Some have argued that the temperate climate of the Holocene encouraged the development of agriculture in some regions (Richerson *et al.* 2001). This in turn led to a population explosion which further encouraged gene flow between regions as groups expanded their home ranges in search of natural resources. For

example, the homogenisation of craniofacial morphology in Europe and the Near East has been linked to the introduction of Neolithic agriculture. In East Asia, a similar process, characterised by the spread of rice-growing agriculturists, is thought to have led to the homogenisation and regionalisation of craniofacial traits (Van Vark and Dijkema 1988). In the case of Europe, some have argued that the spread of gracile craniofacial traits which characterise many Europeans today, were linked to the large scale expansion of Neolithic farmers from the Near East (Sokal and Uytterschaut 1987; Barbujani *et al.* 1995; Pinhasi and Pluciennik 2004; Pinhasi *et al.* 2005). Cavalli-Sforza and Cavalli-Sforza (1995) argued for a similar expansion of Neolithic farmers into Europe from the Near East on the basis of genetic evidence. According to some, the rapid spread of Neolithic farmers led to the complete or partial replacement of (craniofacially diverse) indigenous hunter-gatherer populations in most of Europe and the Near East (Brace and Tracer 1992). This hypothesis is supported by the widespread homogeneity in craniofacial morphology displayed by Europeans compared to greater heterogeneity which apparently existed in these regions prior to the Holocene (Van Vark 1990; Van Vark *et al.* 1992). Recent evidence however, suggests that the genetic contribution of Neolithic farmers to contemporary Europeans, particularly Northern Europeans, may have been smaller than what was previously thought. Instead, according to some, indigenous European hunter-gatherers may have contributed significantly to the phenotype and genotype of most recent Europeans, while the genetic influence of Neolithic farmers may have been restricted to certain regions such as the Mediterranean and parts of Eastern Europe (Haak *et al.* 2005; Brace *et al.* in press).

Although gene flow would have led to a further reduction in genetic and craniofacial heterogeneity in general, similarities between populations would have been largely determined by geographic distance. In regions on the periphery of agricultural developments and major human migrations, such as Australia, recent human populations are not only morphologically distinct, but also display greater long term stability in craniofacial morphology. The appearance of regional cranial characteristics in Australia, date to an earlier time period than in Europe and Asia, and Australian populations appear to have been unaffected by demographic changes in these regions (P. Brown 1987, 1989, 1992). Although some have argued that Pleistocene populations in Australia are morphologically diverse, consisting of robust and gracile populations (Thorne 1977; Thorne and Wilson 1977), more recent research by P. Brown (1987) has indicated that Pleistocene populations may have been quite homogenous. P. Brown (1987) argues that the heterogeneity identified by previous researchers was not due to the presence of two morphologically distinct populations, but was instead related of sexual dimorphism (P. Brown 2000) and the variable occurrence of artificial cranial deformation in Pleistocene populations (P. Brown 1981; Antón and Weinstein 1999). Apart from a reduction in craniofacial dimensions, Holocene Aborigine populations are remarkably similar to Pleistocene Australians in terms of overall craniofacial shape, suggesting a relatively early pre-Holocene date for the occurrence of distinctly Australian craniofacial traits (P. Brown 1987, 1989, 1992). Because of this long-term continuity in Australian craniofacial morphology, some consider Australian Aborigines to be the strongest case for a regional origin of modern humans (Thorne and Wolpoff 1981; Habgood 1989, 1992). It also

shows that craniofacial traits can remain relatively stable for long periods within a population that is relatively isolated from major demographic changes.

CLIMATIC ADAPTATION

Some human populations display differentiation in excess of neutral expectations for certain cranial dimensions (Relethford 2004; Roseman 2004; Roseman and Weaver 2004). The influence of climate and altitude on the human cranium is supported by studies on recent and extinct human populations living in environments with extreme climatic conditions and which appear to have undergone adaptations to those conditions (Coon *et al.* 1950; Guglielmino-Matessi *et al.* 1979; Carey and Steegman 1981; Beals *et al.* 1983, 1984; Franciscus and Long 1991; Relethford 2004; Whitlock 1999; Roseman 2004; Roseman and Weaver 2004). The most compelling evidence in favour of the influence of climatic conditions on the selection of certain aspects of craniofacial shape concerns the shape of the human nose. Nose form is regularly held to be associated with climatic factors because of its link to thermoregulation (Weiner 1954; Crognier 1981; Franciscus and Long 1991). Tall, narrow noses are consistently a feature of populations living in colder environments (e.g. Inuits and Fuegians), while short, broad noses are a feature of populations living in warmer climates (e. g. Khoesan and Negroids) (Collins 1951; Newman 1953; Garn 1965; Hernández *et al.* 1997; Roseman 2004). The distinctive nose shape of Neanderthals is regarded as an adaptation to extremely cold climatic conditions in Glacial Europe (Coon 1962; Schwartz and Tattersall 1996). Evidence for climatic influence on regions of the cranium other than the nose is weak. For instance, it is hypothesised that brachycephalisation (round headedness) is selected for in colder

environments because of thermoregulatory considerations (Guglielmino-Matessi *et al.* 1979; Beals *et al.* 1983, 1984). This is debatable however, since many Inuit have dolichocephalic head shapes, a form which is hypothesised to be less efficient in preserving heat (Harrison *et al.* 1964; Hylander 1977). Facial flatness has also been linked to cold environments (Coon *et al.* 1950). Although the Inuit have flat faces which become flatter with age (Dahlberg *et al.* 1978), Kalahari Khoesan, who live in hot climatic conditions, also have very flat faces (Howells 1989).

Climate may also influence overall craniofacial size. P. Brown (1992) attributed the decline in Aborigine craniofacial size during the early Holocene to a change in climate. He argues that this is the most likely explanation for the decline, since there is no evidence in the Australian archaeological record for the presence of agriculture or the use of pottery cooking vessels prior to European contact. In addition, there is no evidence for gene flow at the time. The reductions in craniofacial size does however coincide with an increase in average air temperature between 8000 BP and 6000 BP. Brown's (1992) hypothesis is supported by other studies which have shown that populations living in warmer climates generally have lower stature levels, lower levels of muscle mass, and smaller, more gracile skeletons compared to people living in colder climates (Hiernaux 1968; Schreider 1975; Roberts 1978; Macho and Freedman 1987). Again, fluctuations in body size probably have to do with thermoregulatory considerations, since Bergmann (1847) and Allen (1877) have noticed a similar trend in animal species with extensive geographic distributions.

CONCLUSION

The patterns of craniofacial variation that characterise many contemporary human populations appear to be relatively recent, post-dating the Pleistocene. Despite the influence of environmental and climatic factors on craniofacial form, the development of modern craniofacial morphology and recent patterns of variation appear to be primarily the result of neutral evolutionary forces. Much of this evidence is based on studies of non-African populations though. Although the deepest genetic roots occur in contemporary sub-Saharan African populations (Templeton 2002, Armour *et al.* 1996; Hammer 1995; Stoneking *et al.* 1997) very little work has thus far been done on the antiquity of the craniofacial morphology of recent sub-Saharan Africans (Henneberg and Steyn 1993). One sub-Saharan African population with some of the deepest genetic roots of all is the Khoesan (Soodyall and Jenkins 1992). Despite more than a century of investigations, we still know very little about the evolution of recent patterns of Khoesan craniofacial morphology. The next chapter reviews the history of studies of Khoesan craniofacial morphology.

CHAPTER THREE

THE HISTORY OF STUDIES OF KHOESAN CRANIOFACIAL VARIATION

INTRODUCTION

The distinctive morphology and the degree of variation exhibited by prehistoric and contemporary Khoesan crania fascinated anthropologists since the late 1800's. Unlike more recent studies however, the aim of these early anthropologists was not to assess morphological variation in order to reconstruct the origins of recent craniofacial patterns, but rather to determine where the Khoesan fell within a perceived hierarchical organization of human "racial types". During the course of the last century, the focus of anthropological interest in the Khoesan cranium changed quite substantially, along with the methods and approaches employed. Anthropologists became interested in the biological origins of the Khoesan and the development of recent patterns of craniofacial morphology. This chapter presents an overview of the history of research of Khoesan craniofacial variation.

EARLY TYPOLOGICAL RESEARCH

Anthropological research in South Africa during the 19th and early 20th centuries, as in the rest of the world, was steeped in the dogma of racial typology (Blumenbach *et al.* 1865; Morton 1839). Essentially, racial typology is concerned with the classification of humans into different "racial" categories. It has its roots in the work of the 18th century Swedish botanist, Carolus Linnaeus, who in 1735 published a landmark book called

Systema Naturae, which helped establish the field of systematics. In the original *Systema Naturae*, and its ten revised versions, Linnaeus presented a new classification for the three kingdoms in nature: the animal kingdom, the plant kingdom and the kingdom of stones. Linneaus also included man in his classification scheme. In the 1758 version of *Systema Natura*, he classified humans into four varieties, namely, Americanus, Europaeus, Asiaticus and Afer. Each variety supposedly had unique physical and behavioural traits that distinguished them from each other.

Linnaeus' (1758) classification scheme of humans did not have any scientific foundation, but was based on then widely held Eurocentric generalisations and assumptions about non-Europeans. By the 19th century, scientists set out to provide Linnaeus' classification scheme of humans with a scientific basis. This led to the development of craniometry, or the study of human cranial dimensions. In 1842, Anders Retzius, an anatomist in Sweden, developed the cephalic index, a method used to describe the shape (as opposed to size) of the human cranium. Because cranial shape was regarded as a stable "racial" trait, it was considered ideal for distinguishing between human, "races". The cephalic index is the ratio of the maximum breadth of the cranium to its maximum length, multiplied by 100. A cranium with an index <75% is referred to as dolichocephalic, or long-headed; a cranium with an index falling between 75% and 80% is referred to as mesocephalic (sometimes mesaticephalic), or medium-headed; and a cranium with an index >80% is referred to as brachycephalic, or short-headed (Stewart 1935). The cephalic index became an important tool to early anthropologists in their attempts to describe and classify human "races" across the world. Relatively unexplored regions such as Africa, Australia and the

Americas proved fertile grounds for scientists who sought to add new groups to the existing list of known human "races".

In South Africa, anthropologists set about the description and classification of South African human populations at a relatively early stage. Western scientific interest in the biology of the Khoesan was officially declared in 1878, when a motion was passed to create a separate Ethnological Section of the South African Philosophical Society, thus establishing anthropology as a formal discipline in South Africa (Tobias 1985). The first major study of Khoesan craniofacial variation was produced by F. C. Shrubsall who published four papers on a large sample of Khoesan crania housed in South African and British institutions (Shrubsall 1898, 1907, 1911, 1922). Shrubsall's samples were not only geographically diverse, but were composed of archaeological specimens as well as crania from contemporary populations. Based on these diverse samples, he concluded that from a craniofacial perspective, the San differed significantly from the Khoekhoe. He described San crania as subdolichocephalic and metriocephalic, while that of the Khoekhoe was dolichocephalic (Shrubsall 1898).

Apart from the San and the Khoekhoe, early researchers also recognised other Khoesan "physical types" in the South African human skeletal record. The origins of each of these "types" were routinely attributed to population migrations. Broom (1923) identified Australoid-like features in a group of Korana crania he was studying. He also described Australoid features on an undated skull discovered at Bayville in the Eastern Cape. A link between Australian and South African populations received further support amongst early scientists with the discovery of an undated cranium on the Cape Flats, near Cape Town

(The Cape Flats Cranium-UCT 98). Staining, accompanied by a robust Australian Aborigine-like morphology that included pronounced supra-orbital ridges, a low frontal bone and dolichocephalic neurocranium, convinced its discoverers that this cranium represented an early common ancestor of South African and Australian populations (Drennan 1929b). On the basis of these crania, it was postulated that an Australoid group had once occupied South Africa (Drennan 1929b). Wells (1942) later pointed out that the Bayville cranium actually shows little resemblance to Aborigines. Singer (1993) also criticised the Australoid concept. He presented a recent cranium that resembles the morphology of the Cape Flats cranium as proof that so-called Australoid morphology is part of the normal craniofacial range of variation present in South African populations (Singer 1993).

One of the most influential "physical types" to be identified in the South African fossil human record was the "Boskop physical type" (Haughton 1917; Broom 1918, 1923, 1929b). Specimens of the "Boskop physical type", also called "Boskopoids", were considered by Broom (1923) to be the direct ancestor of modern San peoples. In recognition of this status, Broom designated this new "physical type" *Homo capensis*. The type specimen of the "Boskopoids" is a large undated skullcap (PEM 120) discovered in 1913 in South Africa's North West Province (then Transvaal Province) (Figure 4.1). According Van Riet Lowe (1954), these remains were discovered at a level at which MSA artefacts also occurred. This association led to the assumption that the "Boskopoids" were the aboriginal MSA peoples of southern Africa (Wells 1959). However, Galloway (1933) argued for a much wider distribution. He saw morphological

similarities between the Nebarara cranium from northern Tanzania and the Boskop skullcap (Galloway 1933). Supposed "Boskopoid" traits were also identified in fossilised crania from the East African sites of Kanjera and Gamble's Cave (Galloway 1937b). By implication, the presence of "Boskopoid" features in these East African crania called into question the indigenous nature of the "Boskopoid" people, and thus that of the San.

The "Boskop physical type" was not based solely on the morphology of the Boskop skullcap, but was a composite form constructed from several crania that were considered to belong to this "physical type" (Dreyer and Meiring 1952). Facial features and other regions of the skull that are absent in the original Boskop skullcap were "reconstructed" based on other fossils (Galloway 1937b). In the end, the "Boskop physical type" came to be represented by an extremely diverse group of crania. Interestingly for the time, Galloway (1937b), who was instrumental in the establishment of the "Boskop physical type", attributed this diversity of morphology to normal variation in "Boskop populations". As more crania were included in the physical type, it became a problematic category that was increasingly difficult to support (Dreyer and Meiring 1952).

Despite the great size of the Boskop skullcap, its pentagonoid shape and its relatively small mastoids and poorly developed supra-orbital ridges lend an almost infantile or foetal form to this cranium. Because of its shape, it was referred to as a paedomorphic type (Wells 1972). Dart (1940) dubbed Boskop a giganto-paedomorph because of its great shape. Paedomorphic traits have been associated with the crania of recent San populations for quite some time (Drennan 1931; Wells 1972). According to Wells (1934),

the San (also called the "Bush physical type" in early literature), is characterised by its small size and markedly infantile form. As in the case of the "Boskop physical type", the "Bush physical type" also possesses slightly developed supra-orbital ridges and small mastoid processes.

These similarities in cranial shape suggested to early workers that the "Boskopoids" and the "Bush physical type" were somehow related in the past. Keith (1935) referred to the "Boskop" and "Bush physical types" as "cousin types". One theory proposed that the "Bush physical type" descended from the Boskop people (Pycraft 1925; Keith 1934). However, this theory could not be supported when it was discovered that the fossil record does not show a neat progression in time from "Boskopoid" to "Bush physical types". Large-headed "Boskopoids" occurred throughout the fossil record along with small-head "Bush physical types". To explain this phenomenon, a second theory was proposed. According to this theory, the "Bush physical type" arrived in South Africa in an already evolved form, intruding on previously established "Boskop types". As well as co-existing throughout history as separate entities, these two "types" also supposedly interbred, leading to "Bush-Boskop hybrids" or "Boskop-Bush hybrids", depending on which "type" dominated in the admixture (Laing 1924; Galloway 1937b). The site of Matjes River Rock Shelter, situated near the Cape south coast town of Plettenberg Bay (Figure 4.1), played an important role in the advancement of a third theory. Louw (1960) distinguished three successive "population types" in this site, each of which corresponded to different cultural levels. According to Louw's (1960) scheme, the oldest inhabitants at the site were Late Pleistocene/Early Holocene "Proto-Bushman" from the site's second

oldest layer, Layer D. The next oldest were the Middle Holocene "Keurbooms (or Wilton) people" from Layer C. Lastly, there were the Late Holocene "Pre-Bushman" people from Layer B. Since the intervening "Keurbooms" crania in Layer C differed quite substantially in form from crania in the upper and lower levels, early workers disputed an ancestor-descendent relationship between the "Proto-Bushman" and "Pre-Bushman types" (Meiring 1937). Meiring (1937) attributed the presence of the "Keurbooms" people to the migration of Palaeolithic populations from North Africa and southern Europe. It was also evident from this site that the Boskopoid-like skulls did not originate in the oldest layers, but in its intermediate and upper layers (Keith 1934; Meiring 1937). This observation placed in doubt suggestions that the "Boskopoids" could have been South Africa's aboriginal MSA population. Within the upper layers, Boskop-like skulls were associated with an array of other forms including "Bush types". Meiring (1937) ascribed this great array of cranial forms, as well as the presence of "Boskop types", to hybridisation between various immigrant populations and local people.

The origins of the Khoekhoe were initially attributed to the hybridisation of "Bush" and "Boskop types" (Drennan 1936; Keith 1934). The site of Oakhurst Rock Shelter near the Cape south coast town of George played a pivotal role in this theory. Drennan (1938) noted that the people in the lower Wilton levels of Oakhurst were significantly taller and more robust than those in the later levels. In this sense, they were said to bear a striking resemblance to the skeletons from the Wilton levels of the Matjes River Rock Shelter. Despite this resemblance, Drennan (1938) argued that the Wilton people from the two sites were not contemporaneous, but that the Oakhurst people represented the more

evolved descendants of the Matjes River people. As evidence for this, Drennan (1938) argued that the presence of pottery in the Wilton levels of Oakhurst, and its corresponding absence in the Wilton levels at Matjes River, suggested a later date for the Wilton at Oakhurst. He also noted that the Wilton people at Oakhurst were not quite so tall, and had slightly smaller crania and longer faces than the Wilton people at Matjes River. According to Drennan (1938), the Wilton people at Oakhurst represented South Africa's Hottentot people just before they acquired their herder culture. Today we know that the Wilton at Matjes River Rock Shelter and Oakhurst Cave is more or less contemporaneous, and that what Drennan (1938) was seeing was simply variation between the two sites (J. Deacon 1984b; Döckel 1998; Wadley 2000b).

Drennan's (1938) take on the origins of the Khoekhoe was heavily criticised by Dreyer and Meiring (1952) who were of the opinion that the Khoekhoe were late immigrants to South Africa. The alleged "Hamitic" appearance of some of the Kakamas material excavated by T. F. Dreyer and A. J. D. Meiring along the Orange River, and their association with conical grave structures which resembled those of East African pastoralists, suggested to these workers that the Khoekhoe had an East African origin (Dreyer and Meiring 1937, 1952). On the basis of these similarities, the Kakamas remains were elevated to the status of "Hottentot type specimens" (Dreyer and Meiring 1937). In addition to supposed East African links, some scientists even extended the genetic roots of the Khoekhoe to beyond Africa, identifying Armenioid, Mediterranean and Mongolian influences in Khoekhoe craniofacial morphology (Dart 1951, 1952).

It is clear that early researchers did not have an appreciation of intra-population variation. If a cranium of unknown genetic affinity did not fit firmly into a "physical type", or it displayed a mosaic of traits, that cranium would be assigned to the status of a hybrid. Today we know that craniofacial variation between major biological populations of *Homo sapiens* is relatively low compared to levels of variation within populations (Relethford 1994). In the past though, crania that did not display one or other idealised morphology, were routinely removed from study samples, thus significantly biasing results (e.g. Salmons 1925; Drennan 1929a; Slome 1929). In the end, scientists were left with categories of crania displaying diverse morphologies. Understandably this led to the conclusion that South Africa was occupied by several diverse "races" of people during the past.

CHANGING APPROACHES AND VIEWS ON KHOESAN CRANIAL VARIATION

Not all anthropologists during the early 19th century accepted that cranial form was unchanging. As mentioned in the previous chapter, American anthropologist Franz Boas was atypical of his generation in the sense that he was more concerned with process and the evolution of individuals, rather than in the construction of "racial" schemes (Gravlee *et al.* 2003). In 1912, Boas stunned an anthropological community still largely steeped in racially motivated studies by reporting marked differences in cranial form between American-born children of immigrants and their European-born parents (Boas 1912a, b). These results finally illustrated that cranial forms can and may change even within a relatively short time. Boas (1940) also heavily criticised the value of the cephalic index.

He argued that it had no biological meaning, and as such, had no descriptive value (Boas 1940). Despite Boas' (1912a, b) evidence for the plasticity of the cranium, it would be decades before there was a complete shift away from typology in anthropological research (P. L. Walker 2000). In South Africa the situation was no different. The first strong evidence for a shift away from typologically driven research occurred during the 1960's with a number of publications suggesting that "race" was too unclear to delineate a study population since it had little biological foundation (W. R. Brown 1958; Livingstone 1962; Brace 1964a, b). These studies argued that an interbreeding population represents a much more biologically sound way of delineating separate human populations. In an interbreeding population, it was further argued, gene flow may be limited by such boundaries as geography, culture and language (Brace 1964a, b).

It was generally assumed during the typological era that the San and the Khoekhoe were biologically distinct "physical types". From approximately the 1960's however, this was not taken for granted any longer. In South Africa, as in the rest of the world, the focus of research had shifted away from typology. Researchers were now interested in determining whether the San and the Khoekhoe were actually different biological entities, and if they where, to what extent they differed. For this type of study, researchers required not only biologically representative samples, but also samples that represented the full range of craniofacial variation of both groups. This would allow them to determine the degree of overlap that occurred. The problem that researchers faced though was how to determine whether a cranium belonged to a San or a Khoekhoe person without using typological criteria. The choice eventually fell on choosing crania on the

basis of cultural affiliation. Attempts to identify the cultural affiliation of skeletal material however, proved extremely difficult, particularly in the case of archaeological skeletons. According to A. G. Morris (1986), scientists scoured museum collections for individuals that were "known-in-life" to have been of either San or Khoekhoe cultural affiliation in an effort to secure representative cranial samples. Typically, identifications in museum catalogues were based on (1) personal testimony from the individual as to what he/she regarded himself/herself as; (2) testimony from the donor of the skeleton that the individual was known to him/her personally as either Khoekhoe or San; or (3) circumstantial evidence that the individual could only have been Khoekhoe or San (A. G. Morris 1986). The cultural affiliations of these so called "known-in-life" skeletons were thus far from secure. In addition, finding a large enough sample for statistical analyses proved harder than was initially anticipated. To get around the problem of small sample size, some researchers supplemented samples with largely undated archaeological skeletons (Rightmire 1970; Howells 1973; Hausman 1980). In a sense, these later studies suffered from similar methodological problems to those experienced by earlier typological studies. Instead of assuming that cranial shape remained unchanged though, they assumed that cultural affiliation remained unchanged. Research at this time was largely based on the assumption that culture and ethnicity were linked (A. G. Morris 1986).

The results of investigations based on samples assembled using the "known-in-life" criteria were almost unanimous in finding very little morphological differences between San and Khoekhoe cranial samples. Based on a sample of 8 male San, 6 female San and 4

Khoekhoe males, Stern and Singer's (1967) preliminary quantitative morphological study indicated that Khoekhoe crania were slightly larger than those of the San. They argued that this reflected quantitatively some of the typical differences that early researchers had subjectively used to distinguish "typical" San crania from those of the Khoekhoe. These include the San's small mastoid processes, small square mandibular ramus, small teeth, shorter face, shorter cranium, smaller orbit heights, and smaller malar bone heights.

Rightmire (1970) produced the first work that employed multivariate statistical methods (discriminant analysis, Penrose's C^2_H and Mahalanobis' D^2 distances) to elucidate issues of Khoesan craniofacial variation. He was able to increase the number of known-in-life individuals for his study from Stern and Singer's (1967) 18, however, his sample was still too small to produce reliable results with the multivariate techniques that he was employing. To increase his sample size, Rightmire (1970) included crania derived from archaeological context in his study sample, a practice followed in subsequent multivariate analyses (e.g. Howells 1973; Hausman 1980, 1982, 1984). Rightmire (1970) found that San and Khoekhoe males were not significantly different from one another, although Khoekhoe skulls appeared to be a little larger in general, particularly in terms of the height of the cranial vault. San and Khoekhoe crania differed significantly from Negroid crania though. Unlike Stern and Singer (1967), Rightmire (1970) found that cranial length did not differ significantly between the San and the Khoekhoe.

In his world-wide survey of human cranial form, Howells' (1973) African sample included a San sample consisting of approximately 90 crania. Of these 20 were derived

from individuals that were "known-in-life", while the rest were derived from archaeological context. Howells (1973) states that his San sample had been excavated from "good Bush country", which by implication suggests that he thought that it was in all likelihood an unmixed population. According to A. G. Morris (1986) though, Howells' (1973) archaeological sample cannot be unambiguously attributed to the San, since there never was a region that had been solely occupied by the San. Howells' (1973) results concur with the results of Stern and Singer (1967) and Rightmire (1970) in that he demonstrated that the crania of San were relatively small in comparison to other populations around the world. Apart from their small size though, the San display a general African pattern, namely very low faces and noses and wide inter-orbital widths.

To date, the most comprehensive study of Khoesan craniofacial evolution had been performed by Hausman (1980, 1982, 1984). She also studied a combination of "known-in-life" individuals and crania from archaeological context. Her sample consisted of 194 crania, which at that stage represented the largest Khoesan cranial sample ever analysed for a single project. Hausman's (1980, 1982, 1984) results broadly agreed with that of Stern and Singer (1967), Rightmire (1970) and Howells (1973) in that she concluded that modern San and Khoekhoe were biologically quite closely related to each other, although Khoekhoe crania were slightly larger. Hausman's (1980) study also represents the first large-scale modern investigation into the evolutionary development of prehistoric and protohistoric Khoekhoe and San populations in South Africa. In a morphological comparison of populations from the Fynbos Biome and populations from the interior of South Africa, she argued that prehistoric Khoesan populations in the Fynbos Biome

displayed very little evolutionary change during the Holocene. On the other hand, populations in the interior appeared to have evolved more rapidly and along a different trajectory to coastal populations. She maintained that her identification of craniometric differences between interior and Fynbos Biome San populations supported an early typological argument that coastal San populations were more "primitive" than inland San populations (Shrubsall 1911). Hausman (1980) also noted that craniometric differences existed between Khoekhoe people in the interior and coastal Khoesan populations in general. This she attributed to the differential spread of the herding lifestyle in South Africa. Not only were coastal regions farther away from the initial point of introduction of domestic stock into the country, but differences in resource distribution between the coast and the interior also determined the degree to which herding became established in these two regions. Hausman (1980) argued further that access to coastal resources caused people on the coast to be more flexible in their subsistence patterns than people in the resource-poor interior. With the introduction of herding, this greater flexibility supposedly countered the establishment of an exclusively herder lifestyle along the coast. In the interior however, people would have embraced herding to a greater extent since herding would have represented a more stable food supply. Acceptance of a new lifestyle, and the accompanying changes in social structure, would in turn have led to the social and economic differentiation of herders from hunter-gatherer communities. With time, this differentiation would have extended to the biological sphere. This argument however, does not take cognisance of the fact that the early ethnography of the Khoekhoe is based on coastal populations in the Fynbos Biome.

METHODOLOGICAL PROBLEMS

The move away from a typological approach and the use of multivariate statistical techniques brought post-typological era scientists closer to defining the patterns of biological variation in recent Khoesan. Unlike earlier typological studies which identified significant morphological differences, these more recent results showed that there were significant overlaps in the morphologies of San and Khoekhoe samples. If there was a difference between these two groups, it was that Khoekhoe crania were generally larger than those of the San. Despite making significant strides in elucidating the actual patterns of craniofacial variation in recent Khoesan populations, the new approach encountered serious methodological shortcomings.

According to Morris (1986) a major problem was the reliability of the ethnic identification of skeletal material in museum registers. There had never been clear criteria by which to classify Khoesan peoples as either San or Khoekhoe (Barnard 1992). In many cases classifications were subjectively made and did not reflect any cultural or biological reality. In addition to this problem, scientists struggled to find large enough cranial samples that would fulfil the known-in-life criterion. It often happened that in an effort to increase sample sizes, due care was not taken in verifying the origins of skeletal material. In this way, genetically mixed samples from medical school dissection halls were inadvertently included in study samples. A. G. Morris (1986) notes that the work by Rightmire (1970) and Hausman (1980) included crania prepared from cadavers in the Department of Anatomy at the University of the Witwatersrand between 1926 and 1957. These were listed as "Hottentot-mixed" or "Hottentot". The reality of the situation was

that by this time, few individuals regarded themselves as either Hottentot or Khoekhoe, and these individuals were more likely to have been of mixed genetic ancestry (A. G. Morris 1986). By including genetically mixed samples, these later studies probably misestimated the actual biological variability of the Khoesan. The inclusion of archaeological samples as a means of increasing sample size may appear preferable to the inclusion of skeletal material of probable mixed genetic origin. However, as A. G. Morris (1986) notes, this practice was problematic as well. Archaeological samples were largely undated when these studies were performed and very few skeletons had clear cultural associations. Sample selections were thus based on unsubstantiated assumptions about cultural association. Both Rightmire (1970) and Howells (1973) chose their archaeological sample of San individuals based on geographic location alone. This practice is groundless since it has never been shown that certain regions were exclusively occupied by the San during the past (J. Deacon 1984b; Schrire 1980; A. B. Smith 1983). Hausman (1980), on the other hand, depended on grave styles to provide cultural affiliations for her archaeological sample. Admittedly, stylistic differences in graves do exist (A. G. Morris 1984; Inskeep 1986), however it is also true that much overlap exists between San, Khoekhoe and Negroid grave styles, making the identification of ethnic affiliation based on grave styles highly dubious (A. G. Morris 1986).

Combining recent and archaeological samples is also problematic for a further reason. This approach ignores temporal changes in morphology and as such prevents a true understanding of the patterns and processes involved in the biological evolution of a population. The failings of this approach are demonstrated in Hausman's (1980)

reconstruction of the biological evolution of the Khoesan during the Holocene. To date, Hausman's (1980) research represents the most extensive post-typology era analysis of cranial variation in protohistoric and prehistoric Khoesan populations. In terms of statistical analyses, her research showed a significant advance compared with the simplistic analyses of typologically based studies. Nonetheless, it still suffered from fundamental methodological and dating constraints. One problem was that she did not factor in the probable effects that temporal change in craniofacial morphology may have had on her study. Granted, with only 19 directly dated crania out of a total sample of 194, Hausman's (1980) ability to control for temporal change was limited. Nevertheless, it was possible to distinguish broadly between recent and archaeological material. However, Hausman (1980) combined recent and archaeological crania into "cultural" subsets, which she then compared on a geographical basis. Based on these combined categories, she argued that prehistoric Khoesan populations in the Fynbos Biome displayed very little evolutionary change during the Holocene. On the other hand, populations in the interior appeared to have evolved more rapidly and along a different trajectory to coastal populations. The morphological differences that Hausman (1980) identified between interior and coastal populations may not be related to geographical differences though. Another explanation could be temporal differences associated with recent gene flow into inland Khoesan populations from other non-Khoesan biological populations. A breakdown of her cranial sample reveals that the vast majority of her interior San and Khoekhoe were either "known-in-life" individuals, or individuals dug up from protohistoric burial grounds. On the other hand, the majority of her Cape Biome sample was derived from archaeological contexts and were probably of prehistoric age. As

previously noted, the genetic histories of "known-in-life" individuals are uncertain, and most, if not all, had been influenced to some degree by genetic mixing with Negroid or Caucasoid populations. In addition, genetic mixing with Negroid populations occurred relatively early in certain regions of the South African interior. A. G. Morris (1984, 1992c) demonstrated that protohistoric Khoesan populations in the Northern Cape experienced substantial gene flow from Negroid populations. Hausman's (1980) interior sample was thus very likely of genetically mixed origin. On the other hand, her coastal Khoesan sample was mainly composed of pre-colonial archaeological material and thus relatively free of the effects of outside gene flow. Negroid farmers avoided the western, south-western and southern coastal regions of South Africa as these regions experienced winter rainfall and were unsuitable for the propagation their summer rainfall crops. In addition, the biological and cultural demise of the original coastal Khoesan populations occurred quite early during the colonisation process. As a result, there are no "known-in-life" Khoesan individuals from these coastal regions.

THE SHIFT AWAY FROM THE KNOWN-IN-LIFE CRITERION

The research carried out by A. G. Morris (1984, 1992c) represents the first recent study of Khoesan craniofacial variation that did not include "known-in-life" individuals. In recognition of the problems involved with this practice, Morris focussed his investigation exclusively on a series of protohistoric period Khoesan burials from the lower Orange River Valley. Unlike previous studies, he employed a few radiocarbon dates measured directly on the skeletal remains, along with archaeological evidence and burial style, to

position his samples in chronological context. In addition to craniometric data, he also employed historical data and ethnographic data to position these skeletons culturally.

A. G. Morris' (1984, 1992c) research investigated the legitimacy of early claims that human remains from Kakamas and other Northern Cape sites represented Khoekoe individuals with East African Hamitic ancestry (Dreyer and Meiring 1937, 1952). In his analysis, A. G. Morris (1984, 1992c) was unable to find any morphological affinities with East Africans. However, he was able to demonstrate that his various samples fell close to the Khoesan centroid, while Kakamas in particular displayed significant gene flow between Khoesan and neighbouring Negroid farmers. Most individuals showed a mix of Khoesan and Negroid cranial traits. A. G. Morris' (1992c) work goes some way towards disproving the hypothesis that the South African Khoekhoe herders had Hamitic ancestry. At the same time, his research also demonstrated that since many protohistoric Khoesan populations from the interior of South Africa displayed significant Negroid admixture, it is unwise to compare them on an equal basis with pre-colonial archaeological samples from the coastal regions of South Africa (as per Hausman 1980, 1982).

DISCUSSION AND UNRESOLVED ISSUES

The significance and origins of the biological variation displayed by recent Khoesan populations still remain unresolved. As discussed above, the biological relationship between the San and the Khoekhoe, and their evolutionary pasts, have been the focus of anthropological enquiry for over a century. Regrettably, early research was hamstrung by a typological approach that placed more stead in dividing Khoesan crania into "physical

types", than on studying intra-population variation or evolutionary development. Because researchers only studied crania that resembled idealised "physical types", information on cranial variation was lost. This resulted in early researchers arguing for the existence of high levels of cranial diversity in the Khoesan. Later researchers took a step in the right direction by shifting the focus of research away from simple typological assessments of cranial morphology, to the assessment of intra-population variation. Study samples were chosen on the basis of cultural affiliation instead of their resemblance to a generalised morphological "type". These studies erred however by assuming that culture and ethnicity were linked and that gene flow did not cross cultural boundaries. The primary aim of research was to determine whether the recent San and the Khoekhoe were biologically distinct populations. Although the assignment of crania to either San of Khoekhoe ethnicity on the basis of culture cannot be considered as secure, these later studies demonstrated that when typological criteria were not used, San and Khoekhoe categories displayed significant degrees of overlap. The only consistent difference between these two categories though, was that crania classed as Khoekhoe were larger than those classed as San. The realisation that the San and the Khoekhoe were actually very similar and were probably only different cultural segments of the same biological population, was a major break from early typological ideas. What was lacking though was information on how recent patterns of craniofacial morphology developed. To date, the most comprehensive analysis of Holocene Khoesan craniofacial evolution was performed by Hausman (1980). Hausman's (1980) study was problematic though because a large part of her sample was undated. She was thus unable to study temporal trends in craniofacial morphology during the Holocene. Since Hausman's (1980) study, there has

unfortunately been no other similarly comprehensive study of prehistoric Khoesan cranial material in the last 25 years. My research thus represents the first recent attempt to investigate the origins of contemporary patterns of Khoesan craniofacial variation using a large sample of dated Holocene crania and modern methods of data collection and statistical analyses. The next chapter (Chapter 4) reviews what we currently know about human craniofacial morphology in South Africa during the Late Pleistocene and Holocene.

CHAPTER FOUR

THE SOUTH AFRICAN MIDDLE STONE AGE AND LATER STONE AGE HUMAN FOSSIL RECORD

INTRODUCTION

This chapter reviews the South African human fossil record for the MSA and LSA. The biological information provided in this chapter, together with the data on technological, subsistence and demographic patterns provided in the next chapter, allows for the construction of hypotheses to test for the origins of recent patterns of Khoesan craniofacial variation. Much of the fossil and sub-fossil material described here has not been included in my analyses because of its fragmentary state. However, it provides an indication of the broad patterns of human craniofacial change that occurred during the South African MSA and LSA. As such, it informs on our current knowledge of the origins of recent patterns of Khoesan craniofacial morphology. The discussion includes MSA human fossil samples such as Klasies River and Border Cave, because these fossils have in the past been identified as possible Khoesan ancestors (Rightmire 1979, 1981; Singer and Wymer 1982). The focus is, however, on the LSA, since this is the period for which we have the best samples and it forms the focus of this thesis. The locations of fossil sites discussed in the text are presented in Figure 4.1.

CONTEMPORARY KHOESAN CRANIOFACIAL MORPHOLOGY

Recent Khoesan populations appear to be quite homogenous in craniofacial shape (Rightmire 1970; Hausman 1980). If anything, Khoekhoe crania are said to be slightly

Figure 4.1: The locations of the major fossil sites discussed in the text.
B: Bushman Rock Shelter
BC: Border Cave
BK: Boskop
CH: Cave of Hearths
EB: Eland's Bay Cave
FL: Florisbad
HM: Hofmeyr
KR: Klasies River
MR: Matjes River Rock Shelter
PC: Peer's Cave
TP: Tuinplaas
WT: Wilton Large Rock Shelter

larger than those of the San (Stern and Singer 1967). Intra-population craniofacial differences in the Khoesan have to be treated with caution though, for reasons discussed in Chapter 3. More pertinent than the craniofacial differences between the San and the

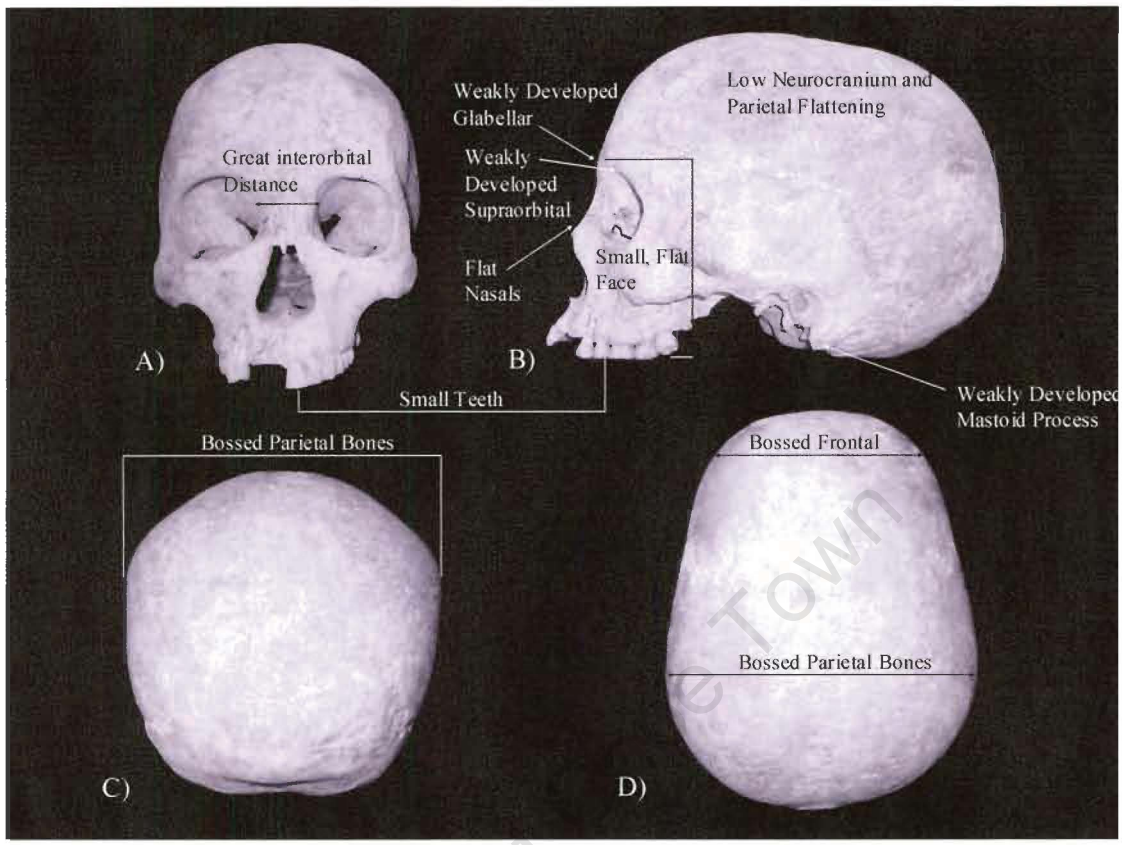

Figure 4.2: Typical Khoesan craniofacial features. The cranium belongs to a male (SAM-AP 6313b).

Khoekhoe though, are the morphological differences that distinguish the Khoesan as a whole from neighbouring African populations such as the Negroids. According to Bräuer and Rösing (1989), the most distinguishing feature of Khoesan crania are their paedomorphic or infantile appearance. Morphological attributes of paedomorphism include the following: bossed frontal, parietal and occipital bones, resulting in a pentagonoid outline to the neurocranium in the superior view; low neurocrania and parietal flattening; weakly developed mastoid processes, glabellar and supraorbital regions; small flat faces resulting from steep frontals, flat nasals, and faces that are small relative to the neurocranium; great interorbital distances; small teeth and gracile mandible

(Figure 4.2) (Tobias 1957; Schwidetzky 1969; Bräuer and Rösing 1989). Craniofacially, Negroids are not paedomorphic, possessing long, narrow neurocrania and prognathic facial features (de Villiers 1968). It should, however, be remembered that these morphological distinctions are not absolute. Overlaps in morphology do exist. Besides late Holocene gene flow between these populations, overlaps in morphology are probably also due to the Khoesan and Negroids sharing a common African ancestry (Bräuer and Rösing 1989).

SKELETAL MATERIAL FROM MSA CONTEXT

There is abundant cultural evidence for the presence of substantial human populations in South Africa during the MSA (Beaumont 1978; Voleman 1981; Singer and Wymer 1982; H. J. Deacon and Geleijnse 1988; H. J. Deacon and Schuurman 1992; G. Avery *et al.* 1997; Henshilwood *et al.* 2001; Marean *et al.* 2004). In contrast, human remains are extremely scarce. The paucity of the MSA human fossil record can probably be explained by a lack of burial practice amongst South African MSA people. In Europe, where Neanderthal skeletal remains are relatively common, the ritual interment of the dead in caves helped preserve their skeletal remains. In contrast, MSA human remains found in South African caves appear to have been treated very differently. Remains are normally very fragmentary, and often only teeth remain. In the case of Klasies River, human bones are not only fragmentary, but a few display cut marks (Singer and Wymer 1982). In this section I will review the MSA fossil material that is of relevance to the current study. The review proceeds roughly in order of decreasing age of the fossil material.

FLORISBAD

The Florisbad skeletal material was discovered by G. Venter and T. Dreyer in 1932 in a spring deposit on the farm of Florisbad, about 45 km NW of Bloemfontein (Dreyer 1935). Dreyer (1935) indicated that the fossil material originated at the level of the lowest of three peat layers, Peat 1. Apart from extensive faunal remains, this level also contained lithics of general MSA type (Dreyer 1935). An early radiocarbon date of 43 700 BP (Pta 3465) indicated that the Florisbad fossil remains lay beyond the limits of radiocarbon dating. A U-series date on the peat layer in which the fossil was found, indicated a date in excess of 100 000 years. Grün *et al.* (1996) performed ESR dating directly on the molar. They reported a weighted mean age of 259 000 ± 35 000 years (Grün *et al.* 1996).

The skull was initially reconstructed by Dreyer shortly after its discovery (Clarke 1985). In his description of the fossil, Dreyer (1935) emphasised its uniqueness compared to other fossil *Homo sapiens*, by assigning it the new species name *Homo (Africanthropus) helmei*. Drennan (1935, 1937) emphasised its resemblance to Neanderthals, and proposed re-naming it *Homo florisbadensis (helmei)*. Galloway (1937a) argued that it resembled modern populations, and in particular, "Australoids" or indigenous Australians. More recent descriptions have emphasised its similarities to other archaic African fossils such as Kabwe and Saldanha (Singer 1958; Tobias 1968; Rightmire 1978a). All these descriptions may, however, be incorrect, since Clarke (1985) reported that Dreyer's reconstruction of the Florisbad cranium had been faulty. Clarke (1985) performed a more accurate reconstruction, giving Florisbad a broad palate and large nasal cavity. Schwartz and Tattersall (2003) note that the face of the latest reconstruction is large and archaic in appearance, with frontal bones that slope gently superoposteriorly. The supraorbital

margin is thick, but it does not form a supraorbital torus. The calotte is thick, with its greatest thickness at bregma. Rather than resembling modern populations, Clarke (1985) argues that the new reconstruction closely resembles archaic *Homo* fossils such as Ngaloba and Omo 2. It also shows a strong resemblance to Kabwe, but appears to be more advanced in certain aspects (Clarke 1985).

KLASIES RIVER

The Klasies River MSA fossils consist of approximately 30 fragmentary cranial and postcranial bones from a series of wave-cut caves on the south coast of the Western Cape Province. This material was recovered in two excavations, the first led by Singer and Wymer from 1967 – 1968 (Singer and Wymer 1982), and the second by H. J. Deacon from 1984 – 1989 (Rightmire and H. J. Deacon 1991; Braüer *et al.* 1992). The initial descriptions of the Klasies River hominid material was performed by Singer and Wymer (1982).

The fossils are not all of a single age, but were scattered throughout the MSA deposits. The majority of the fossils have now been reliably dated to between 90 000 and 120 000 years ago (H. J. Deacon *et al.* 1988; Grün *et al.* 1990). The oldest are two *ca.* 120 000 year old maxillary fragments found since the resumption of excavations in 1984 (Braüer *et al.* 1992). Additional cranial fragments include an almost complete mandible, mandibular fragments, mandibular and maxillary teeth, a piece of frontal bone including the glabella and several parietal fragments. The fragmentary nature of the fossils is of particular interest. The pattern of breakage, as well as the presence of cut marks and

burning on some bones is suggestive of cannibalistic activity (White 1987, 1992; Rightmire and H. J. Deacon 1991).

Singer and Wymer (1982) were the first to suggest that there may have been biological continuity between the Klasies River people and LSA South African populations. They note that the Klasies River fossils display a generalised Negroid morphology, as might be expected in the ancestors of modern Negroid and Bushmen people (Singer and Wymer 1982). H. J. Deacon (1989) later expanded on the idea of biological continuity between MSA people like Klasies River and later LSA peoples. On the basis of archaeological evidence, he argued that human populations along South Africa's southern coast may have developed in isolation from other African populations since the MSA. Recent prehistoric and early colonial Khoesan populations may thus trace their biological ancestry back to MSA people like Klasies River. Morphological links between Klasies River and recent LSA populations are however difficult to establish. A. G. Morris (1992b) has argued that the MSA human sample is too small and fragmentary to demonstrate morphological continuity with LSA populations. Apart from the sample issue however, there are also questions around the modernity of the Klasies material. Although the Klasies River fossils have often been held up as representing some of the earliest evidence for the presence of anatomically modern humans in Africa, the modernity of the Klasies fossils are not beyond doubt. Opinions have varied greatly about the anatomical modernity of these fossils. Singer and Wymer (1982) have argued that the Klasies River hominids were fully anatomically modern. Braüer (1984), Rightmire and H. J. Deacon (1991) and Braüer *et al.* (1992) have agreed with Singer and Wymer's (1982) opinion

that the Klasies River people were essentially modern. Others such as Caspari and Wolpoff (1990), Frayer *et al.* (1994), Lam *et al.* (1996) and Wolpoff and Caspari (1996) have argued that the Klasies River fossils are not modern. Lam *et al.* (1996) note that the low frequency of pronounced chins in the Klasies River sample is very unlikely to be found in any recent human population. Even Singer and Wymer (1982) note that the most primitive mandibles resemble the Cave of Hearth specimen (discussed below) and differ markedly from modern South African Negro specimens. Additional archaic traits include marked supercilliary development, broad interorbital distances, the lack of bipartite brows, and large facial dimensions (Wolpoff 1992; Schwartz and Tattersall 2003). The Klasies River fossils also display great variability in size, particularly with regards to mandibles and dentition. It has been suggested that this great variability is indicative of the high level of sexual dimorphism that characterised the Klasies River people, a trait that was common in archaic populations (Rightmire and H. J. Deacon 1991).

BORDER CAVE

The Border Cave MSA series originates from a cave in the Lebombo scarp, on the KwaZulu/Natal side of the international border with Swaziland. The partial cranium, BC 1, was found during guano digging activities by W. E. Horton in 1940 (de Villiers 1973). Subsequent excavations by H. B. S. Cooke, B. Malan and L. Wells in 1941-1942 uncovered BC 2, a partial and edentulous mandible, in the dumps of the guano miners, and BC 3, a partial infant skeleton in an excavation of undisturbed sediments (de Villiers 1973). Excavations by P. Beaumont in 1974 uncovered a second adult cranial specimen, BC 5, a partial mandible with four teeth (Grün *et al.* 2003). Postcranial remains and a pair of femoral and tibial shafts had also been discovered early on (H. B. S. Cooke *et al.*

1945). However, these have since gone missing (de Villiers 1973). In 1987, four additional postcranial remains were discovered during section cleaning by P. Beaumont (A. G. Morris 1992b).

Uncertainties surrounding the stratigraphic provenance of the Border Cave MSA specimens have hindered attempts to date them. The ages for BC 1 and BC 2 are most uncertain, because these specimens were found in disturbed contexts. BC 3 and BC 5 may have been intrusive burials and thus younger than the units in which they were found (Sillen and A. G. Morris 1996). Beaumont (1980) nonetheless has argued that BC 1-3 and BC 5 derive from levels in the cave that had been dated by ESR to between 80 000 and 55 000 years. A recent direct ESR date of 74 000 ± 5000 on tooth enamel appears to support an early date for at least BC 5 (Grün *et al.* 2003).

According to initial descriptions of the Border Cave material (Cooke *et al.* 1945; Wells 1959; de Villiers 1973, 1976), BC 1 has much of its frontal region preserved and a smaller part of its parietal. It also has part of the right orbit and zygomatic preserved. The cranium is that of an adult, probably male, individual. Although there is no pelvis to confirm the sex, de Villiers (1973) notes that the robusticity of the cranial vault bones, the presence of superciliary eminences, a marked supramastoid crest, and the presence of muscular markings on the squamous portion of the occipital suggest that BC1 is male. In lateral view, the frontal is of moderate height and recedes slightly. In anterior view, the frontal is wide, however, it displays little bossing. The cranial vault is incomplete, but appears to have been long and of moderate height. The parietal contours are moderately

CHAPTER ONE

INTRODUCTION

FOCUS OF THE THESIS

The biological evolution of the Khoesan of southern Africa remains poorly understood, in stark contrast to their much better known cultural record. This imbalance in knowledge is, however, not surprising. A sizable majority of prehistoric human remains from South Africa represent individual interments, making it difficult to extract biological information about the populations from which they derive. Additionally, this sample is geographically, temporally, and in certain cases genetically, diverse. However, the single most important impediment to research into origins of these peoples has been the lack of a large representative sample of dated remains. This dissertation reports on a craniometric analysis of a large sample (n = 153) of recently dated Later Stone Age (LSA) human crania from South Africa's western, south-western, southern and south-eastern coasts and coastal forelands. It explores morphological similarities and dissimilarities within this geographically and temporally diverse sample. In particular, it addresses the questions of how much variation existed and whether the cranial series represents a single population or derives from several distinct populations. It also identifies the major sources of variation. Ultimately, this research has a bearing on two issues: (1) the origins of recent patterns of Khoesan craniofacial morphology; and (2) the question of population continuity in the South African LSA, an issue that has proven difficult to address in archaeologically based studies.

bossed (de Villiers 1973). BC 2 consists of most of the mandibular corpus and part of the right ascending ramus. The corpus is of moderate height and robusticity. The symphyseal region presents a well-developed mental protuberance (de Villiers 1973). BC 5 consists of the entire right mandibular corpus and part of the right ascending ramus, and a quarter of the left corpus. Schwartz and Tattersall (2003) describe this mandible as small and lightly built. They further note that there is not a well-developed mental protuberance, but there is a swelling across the anterior inferior symphysis. There is also no detectable central keel, which according to Schwartz and Tattersall (2003) suggests that the MSA Border Cave remains were not totally modern.

Despite Schwartz and Tattersall's (2003) comments about the lack of a central keel on BC 5, most researchers who have studied the Border Cave remains agree that they are anatomically modern. Opinion is however divided on whether they resemble modern African populations. In the first detailed description of BC 1, de Villiers (1973) argued that it could be differentiated from all living southern African populations. Later, a detailed statistical study could not significantly distinguish the two mandibles, BC 2 and BC 5, from either Khoesan or Negroid samples (de Villiers 1976). Rightmire (1979, 1981) was the first researcher to assign BC 1 to a specific contemporary population when it correlated most closely with his "Hottentot" reference sample. This result was later contradicted by de Villiers and Fatti's (1982) study which assigned BC 1 to membership of an early population that displayed Negroid affinities. The most recent studies have brought research on the Border Cave specimens full circle with results indicating that

they display no affinities to any extant population (Ambergen and Schaafsma 1984; Van Vark 1986).

CAVE OF HEARTHS

In 1947, B. Kitching found the Cave of Hearths mandibular fragment in a cave by the same name in the Makapansgat Valley, Limpopo Province. The mandible has not been securely dated but is probably of late Pleistocene origin. According to J. D. Clark (1964), the fossil originated from the cave's Acheulean levels. However, Mason (1962) supported a late Pleistocene date. Later Oakley *et al.* (1977) reported a date of >16 000 years for the MSA level overlying the level in which the fossil had been discovered. The fossil consists of a right mandibular corpus without its ascending ramus. Early researchers have identified both Neanderthal traits (Dart 1948) and *Homo erectus* traits (Tobias 1968, 1971). In a more recent description, Schwartz and Tattersall (2003) note that this fossil has a moderately developed chin, an archaic trait displayed by other late Pleistocene South African fossils such as Klasies River and Border Cave.

SKELETAL MATERIAL FROM THE MSA/LSA TRANSITIONAL PERIOD

Human skeletal remains from the MSA/LSA transitional period are just as rare as remains from earlier in the MSA. In addition to being rare, skeletal remains from this period are generally not securely dated, but have been assigned to the MSA/LSA transitional period based largely on circumstantial evidence. This sample includes some historically important cranial material such as the Boskop cranium, which has played an integral role in early theories about Khoesan origins. Regardless of being temporally

dubious, this group will be reviewed because of their historical significance to the debate on Khoesan origins.

HOFMEYR

The Hofmeyr cranium was discovered in 1954 in the Hofmeyr district in the Eastern Cape Province of South Africa. The specimen has not yet been fully published at the time of the writing of this thesis, but research results have been presented at two conferences. An OSL date of 36 400 years before present has been generated for the compacted soil infill of the cranium. With an error of roughly 6000 years, this places the date of the Hofmeyr cranium between *ca.* 30 000 and 40 000 years ago (A. G. Morris *et al.* 2005).

A. G. Morris and Grine (1999) have described the morphology of this fossil as a mosaic of archaic and modern traits. The zygomatic region is described as modern, as is the steeply rising frontal and the general form of the cranial vault. The supraorbital and midfacial regions have been described as archaic (A. G. Morris and Grine 1999). A. G. Morris *et al.* (2005) report that the Hofmeyr cranium falls outside the range of variation displayed by modern Khoesan crania in most aspects of craniofacial morphology. Instead, analyses of facial dimensions and vault curvature situate the Hofmeyr cranium within the range of variation of European Upper Palaeolithic crania.

BOSKOP

The Boskop fossil material was found in 1913 by workers digging a trench at the open air site of Koloniesplaats, on the east bank of the Mooi River, in the North West Province (Haughton 1917). The Boskop specimen, which consists of a calotte, temporal and

mandibular fragments, and some postcranial remains, represents the first fossilised human material found in South Africa. Boskop has had a major impact on early theories of Khoesan origins in the past, as it was viewed as a representative of the original MSA occupants of South Africa.

The age of this specimen is extremely uncertain. According to Van Riet Lowe (1954), these remains were discovered at a level at which a single MSA artefact had also been found. An early description by Haughton (1917) indicated that the fossil had been found in a layer of brecciated river sediments consisting mostly of cemented ironstone pebbles. The stratigraphic contexts of the fossil and associated faunal and artefactual remains are not secure, and the material appears to have been secondarily re-deposited by river action. A late Pleistocene date is supported by elemental analyses (Oakley *et al.* 1977).

As described by Wells (1934), the original Boskop skullcap is extremely large in comparison to most Khoesan crania. Apart from its size, the original Boskop calotte is not much different from the crania of recent Khoesan populations. With a narrow frontal breadth and a wide parietal breadth, the Boskop neurocranium is markedly pentagonoid in shape when viewed superiorly. The neurocranium is flattened on top when viewed laterally. The mastoid processes are relatively small and compressed. The supra-orbital ridges are not well developed (Wells 1934). Despite the great size of the Boskop skullcap, its pentagonoid shape and its relatively small mastoids and poorly developed supra-orbital ridges lend an infantile or foetal form to this cranium. Because of its shape, Wells (1972) referred to it as a paedomorphic type. As previously mentioned,

paedomorphism had also been associated with the crania of modern Bushman or San populations (Drennan 1931; Wells 1972). The similarity of the Boskop calotte to recent Khoesan crania suggests that it probably post-dates Hofmeyr, which displays no morphological association to recent Khoesan peoples. This suggests that Boskop may date to the terminal Pleistocene.

TUINPLAAS (SPRINGBOK FLATS)

Tuinplaas was discovered in 1929 in a quarry in the Northern Province by C. J. Swierstra and H. Lang. The skeletal material consists of a fragmentary cranium, a mandible and assorted postcranial bones. No artefacts were found with this specimen, but the remains of an extinct buffalo, *Homoioceras bainii*, was found at the site in subsequent excavations (Broom 1929a).

Early researchers have assumed that Tuinplaas dates to the MSA because *Homoioceras bainii* fossils had been found in association with MSA stone tools at a site in the Free State (Broom 1929a). Wells (1959) has hypothesised that the cranium dates to the end of the Pleistocene. Radiocarbon analysis of the calcareous crust covering the bones produced a minimum date of 5570 ± 100 BP (Pta-256) (Vogel and Marais 1971). Direct radiocarbon analysis of the specimen produced an anomalously young date of 690 ± 90 BP (OxA- 4279) (Pike *et al.* 2004). The $\delta^{13}C$ value of -26.6 ‰ does not fit the expected range for bone collagen, suggesting that the sample was probably contaminated (Hedges *et al.* 1996). Recently U-series dates measured directly on the specimen, using laser

ablation mass spectrometry, pegged Tuinplaas to between 11 000 ± 700 and 20 000 ± 3000 years (Pike *et al.* 2004).

Despite its fragmentary nature, it is clear that the Tuinplaas cranium was large and ovoid in shape. Areas that are well-developed include the supraorbital region and mastoid processes. The mandible is large and robust (Braüer and Rösing 1989). The postcranial remains suggest a tall and muscular individual (Wells 1947; Pfeiffer *et al.* 1996). All these features point towards Tuinplaas being male. The fragmentary nature of Tuinplaas has led to diverse interpretations about its population affinities. The first reconstruction and brief description of the cranium was by Broom (1929a). Galloway (1937c) performed another reconstruction and suggested that Tuinplaas was a member of the Boskop physical type. Galloway's (1937c) assessment of Tuinplaas as a Boskop type was echoed by Schepers (1941) and Wells (1959). Tobias (1959) however notes that, unlike the Boskop cranium, Tuinplaas is a non-paedomorphic type. Later analyses identified a mixture of Negroid and San features (Toerien and Hughes 1955) as well as European traits (Cole 1954). More recent analyses have placed Tuinplaas within the distribution of male Negroids (de Villiers and Fatti 1982). Hughes (1990) also identified morphological associations with Negroid populations. Although these studies have hypothesised that the morphological similarities between Tuinplaas and Negroid crania suggest that Negroid populations might have been in South Africa prior to the introduction of the Iron Age during the last 2 millennia, these claims have not received wide scale acceptance. It is likely that Tuinplaas only resembles recent Negroid populations in terms of size and

robusticity. More importantly in the context of this study, Tuinplaas does not display typical Khoesan craniofacial features, but is of a more generalised African type.

BUSHMAN ROCK SHELTER

The Bushman Rock Shelter skeleton, which consists of a mandible and fragmentary postcranial skeleton of a juvenile, was discovered in 1969 in Mpumalanga Province. The site contains MSA and LSA archaeological deposits. C14 dates for the levels in which the skeleton was found suggest an age of between *ca.* 27 000 – 31 000 years BP (Protsch and de Villiers 1974). A much later date of between *ca.* 12 500 – 10 000 years BP was suggested by de Villiers and Fatti (1982).

de Villiers (1979) notes that the cranial vault had been crushed and provides no useful information. Visual and metric comparisons of the mandible with like-aged San and Negroid specimens suggest that the Bushman Rock Shelter specimen has a closer affinity to Negroids. It is not only larger than like-aged Khoesan mandibles, but also possesses none of the morphological features associated with the Khoesan (Protsch and de Villiers 1974; de Villiers 1979; de Villiers and Fatti 1982). Again, as in the case of Tuinplaas, the association with Negroid populations is not widely accepted. Rather, like other late Pleistocene specimens, Bushman Rock Shelter appears to display generalised African craniofacial characteristics.

CAPE FLATS

The Cape Flats cranium was discovered in quarry works in Philippi, Cape Town in 1929. Goodwin (1929), who visited the quarry soon after the discovery, pointed out that

artefacts of both Still Bay (MSA) and Wilton types were discovered in the dump which yielded the Cape Flats cranial fragments. There is thus no way of determining whether the cranium had been associated with either MSA or LSA tools. Goodwin (1929) could not rule out the possibility that the cranium originated near the surface and may thus be of historical age. A. G. Morris (1992d) provided a recent date of 150 ± 50 BP on an "associated femur bone", although the association with the Cape Flats cranium is questionable. It is possible that the femur belonged to another, probably much younger cranium, found along with the Cape Flats cranium. Unlike the Cape Flats cranium which does not display typical cranial features associated with recent San, the other, more fragmentary cranium was described by Drennan (1929b) as possessing obvious San features.

The Cape Flats cranium attracted the attention of early researchers because of its large size and great robusticity, resulting in a resemblance to European Pleistocene fossils such as Brno (Braüer and Rösing 1989). The most striking feature of this cranium is its pronounced supraorbital ridges, resulting almost in a *torus orbitalis* (Drennan 1929b). It also has a marked post-orbital depression and a sloping forehead. The neurocranium is relatively long and narrow. Drennan (1929b) noticed resemblances to Negroid and European populations in the facial region. However, he felt that the most striking resemblance was with Australian aborigines. As mentioned above, the Cape Flats cranium has not been dated. However, the fact that it does not resemble the crania of recent Khoesan populations, suggests that it might pre-date the origins of recent patterns of Khoesan craniofacial morphology.

SKELETAL MATERIAL FROM THE LSA

The prehistoric South African human skeletal record is most complete during the Holocene LSA. It is during the early Holocene that concrete evidence of the intentional interment of the dead occurs for the first time. From then on, ritual interments, particularly in caves, started to increase gradually throughout the Holocene (Hall and Binneman 1987; Hall 1990). This had the positive side-effect of an increase in the incidence of well-preserved human skeletons. A peak in the incidence of human remains is reached after *ca.* 4000 BP, when population density increased markedly from earlier levels, and the practice and ritual aspects of human burial were well established (Hall 1990, 2000). The South African Holocene human skeletal record, like the archaeological record, is most complete along the southern coast of South Africa. Long term climatic and environmental stability during the terminal Pleistocene and Holocene, were conducive to long term population growth in these regions (J. Deacon 1984b; Hall 2000). The rest of the country, particularly the interior, was only sporadically occupied due to climatic variability (J. Deacon 1984b). Consequently, the human skeletal record in the interior was practically nonexistent prior to the late Holocene (A. G. Morris 1992d). In this section I will review the South African human skeletal record for the LSA.

TERMINAL PLEISTOCENE (*ca.* 16 000 – 10 000 BP)

There are currently no firmly dated human skeletons dating to the early part of the LSA. However, some of the specimens described in the section on the MSA/LSA transition may well date to this time. For instance, the new U-series dates on Tuinplaas situate the age of this individual in the terminal Pleistocene. However, more dates are required.

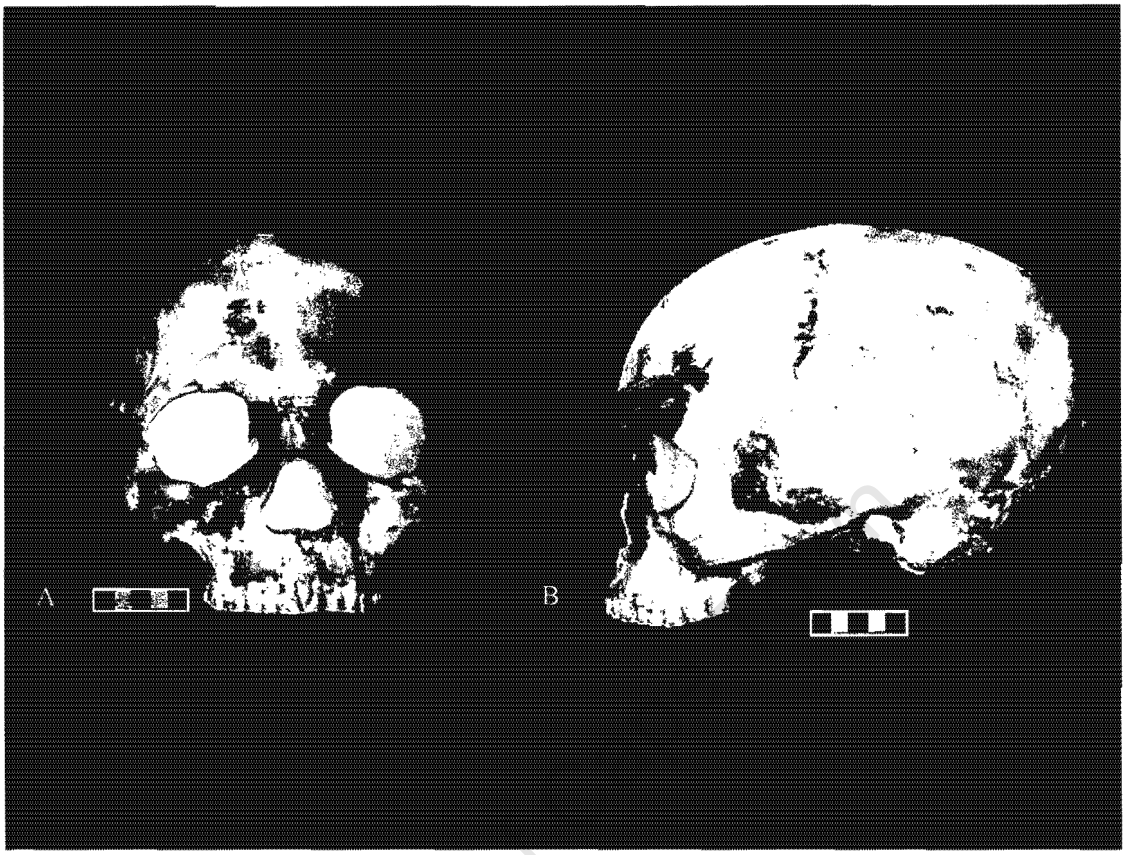

Figure 4.3: The Fish Hoek (Skildergat) cranium (original cast). A) Anterior view. B) Lateral view.

There is currently only one specimen, the Fish Hoek skeleton, which can be assigned to the terminal Pleistocene with relative certainty. Fish Hoek is important since it is the first pre-Holocene cranium to display a significant resemblance to recent Khoesan populations.

FISH HOEK (SKILDERGAT)

Fish Hoek (Figure 4.3) was discovered by V. Peers and B. Peers in a rock shelter (alternatively known as Peers' Cave or Skildergat) in Fish Hoek, Cape Town, sometime in the 1920's. The material consists of the cranial and postcranial remains of a male individual, and the skeleton is practically complete.

The Peers' discovered several skeletons at the site. All but one (SAM-AP 4692) were clearly from LSA levels. B. Peers described SAM-AP 4692 as coming from the late MSA levels in the cave (Peers and Goodwin 1953). In reality, excavation techniques were crude at the time, and Peers could not tell whether SAM-AP 4692 was buried in the MSA levels, or whether it was an intrusive LSA burial. An indirect age of between 35 000 and 36 000 years BP was arrived at by the analysis of charcoal that originally underlay the burial (Anthony 1967; Vogel and Beaumont 1972) and fauna that may possibly have been associated with the fossil (Protsch 1974). It is probable that this date vastly overestimates the age of Fish Hoek. A radiocarbon date has been obtained on post-cranial bone of this specimen, but has thus far not been published, and is not available for citation. Reliable sources report that it is *ca.* 12 000 BP. This is consistent with the stratigraphic provenance of the skeleton (J. Deacon and Wilson 1992). The date has recently been corroborated by unpublished results from C:N analysis which indicate that SAM-AP 4692 has C:N values similar to those of non-human bone from post-MSA layers at Peer's Cave (Yates pers. comm.). C:N ratios track the degree of protein preservation in the bone, and can be used as a relative dating tool within a stratigraphic sequence. There is thus sufficient evidence to be confident that this specimen is in fact *ca.* 12 000 years old.

SAM-AP 4692 is a large cranium. Schwartz and Tattersall (2003) describe the neurocranium of SAM-AP 4692 as long, low and rounded. The face is small and tucked under the frontal. The mid-facial region is broad and flat. Viewed laterally, the frontal (which has a low keel) rises steeply from a minimally swollen glabella up to a posteriorly

placed bregma, and then descends gradually. Viewed from the posterior, the neurocranium bulges low down, reaching its maximum width just above the level of the parietomastoid suture. The mandible is small and gracile. Interestingly there is no keeling of the symphysis (only a broad median swelling), resulting in a chin region that is not very pronounced. The mandible also has a retromolar space (Schwartz and Tattersall 2003). Schwartz and Tattersall (2003) note that these features on the Fish Hoek mandible are conventionally regarded as archaic traits. Most researchers who have analysed the cranium of SAM-4692 agree, though, that it bears close resemblance to recent Khoesan populations (Keith 1931; Howells 1969; Rightmire 1974, 1978b). In Howells' (1973) analysis, SAM-AP 4692 appears as least distant from his Bushman sample. Analysis by Van Vark (1984) however, removes SAM-AP 4692 from all modern populations and positions it closest to Upper Paleolithic crania such as Předmostí 4.

EARLY HOLOCENE (*ca.* 10 000 BP – 7000 BP)

The early Holocene provides the first concrete evidence for the systematic interment of the dead. Evidence of ritual activity is evident at Matjes River, where burials contain substantial amounts of ochre and some ostrich eggshell beads (Louw 1960). It is thus not surprising that there is a significant increase in the number of human remains during the early Holocene compared to earlier periods. Archaeological sites that have produced early Holocene human remains include Wilton Large Rock Shelter (Hewitt 1921; J. Deacon 1969, 1972; F. B. Silberbauer 1979) in the eastern region; Oakhurst Cave (Drennan 1938; Goodwin 1938; Patrick 1989), Van Bonde's Cave (Sealy and Pfeiffer 2000), Drury's Cave (Shrubsall 1922; Roux 1980; Sealy and Pfeiffer 2000), Tucker's

Cave (Sealy and Pfeiffer 2000) and Matjes River Rock Shelter (Louw 1960; Protsch and Oberholzer 1975) in the southern region; and Elands Bay Cave (Parkington 1981; A. G. Morris 1992a; Braüer and Rösing 1989) in the western region. Unfortunately, very little is known about the craniofacial morphology of human populations at this time. The fragmentary nature of many of the early remains, as well as a lack of dated specimens, have thus far inhibited researchers from building a more complete picture. The crania that have contributed most to our current (limited) knowledge of early Holocene craniofacial morphology are UCT 378 and UCT 374 from Elands Bay Cave (Braüer and Rösing 1989), various fragmentary crania from early Holocene layers at Matjes River Rock Shelter (Louw 1960; Protsch and Oberholzer 1975), and ALB 119 from Wilton Large Rock Shelter (Braüer and Rösing 1989). As a group, these fossils share many similarities including low, broad faces which resemble those of recent Khoesan populations. Like many other early Holocene populations around the world (P. Brown 1987, 1992), these South African crania also display heightened levels of robusticity (Bräuer and Rösing 1989).

ELANDS BAY CAVE

Elands Bay Cave produced two fragmentary early Holocene crania during systematic excavations at the cave in 1978 (Parkington 1981). These specimens are UCT 378 (Albany man) and UCT 374 (Ursula). UCT 378 yielded a date of 10 860 ± 180 BP (OxA-478), and is the older of the two. UCT 374 is almost a thousand years younger, dating to 9750 ± 100 BP (Pta-3086).

Although these specimens had been reconstructed by A. G. Morris and a preliminary analysis performed, very little has been published on them. Of the two crania, the morphology of the more complete UCT 378 is better known. A. G. Morris (1992a) reports that this cranium is that of a male that was probably not more than 40 years old when he died. Braüer and Rösing (1989) note that like the Cape Flats and Fish Hoek crania, UCT 378 is quite robust. Its neurocranium is long and low, and lacks prominent parietal bosses. The frontal region slopes gently backwards. Supraorbital development is moderate to strong. The mastoid processes are large and strongly developed. The face is low and broad. The nasal aperture is particularly broad and the orbits low (Braüer and Rösing 1989). Braüer and Rösing (1989) note that UCT 378 resembles recent Khoesan populations particularly in the face, but diverge from these populations in terms of its greater robusticity. UCT 374 has thus far not been described.

MATJES RIVER ROCK SHELTER

Matjes River Rock Shelter was first excavated by T. F. Dreyer in 1928 (Dreyer 1933). Subsequently, further excavations and studies of material were carried out by Meiring (1937, 1953), Hoffman (1958), Louw (1960) and H. J. Deacon and Döckel (Döckel 1998). In his initial description of the site, Dreyer (1933) distinguished five stratigraphic layers, Layers A – E, with E being the oldest and A the youngest. The oldest date for the site is *ca.* 11 000 BP (Hoffman 1958). Human remains occur practically throughout the sequence at Matjes River. Unfortunately the potential of this site as a record of morphological change in South African Holocene populations was lost early on. Excavation methods were very crude. Not only are the fossils extremely fragmentary, but the stratigraphic provenience of individual fossils are in many cases uncertain, and the

lack of proper excavation notes makes it impossible to reconstruct the provenience of skeletons accurately.

The oldest human remains from the site derive from Dreyer's Layer D. Radiocarbon dates place the age of this layer between *ca.* 11 000 and 7500 BP (Louw 1960; Protsch and Oberholzer 1975; Döckel 1998). Observing that early human remains from Layer D were larger and more robust than those in the younger layers, Dreyer (1933) assigned them to a new human subspecies, *Homo sapiens dreyerensis*. Dreyer (1933) later changed his mind but still called the Layer D specimens the "Matjes River Race". Hoffman (1958) suggested the term "Proto-Bushman" for the material from Layer D. Very few of the Layer D skeletons have been directly dated, and unfortunately some of the results for those that were dated are unreliable. In these cases, Protsch and Oberholzer (1975), who were the first to date Matjes River human skeletal material, had combined bones from more than one individual, resulting in meaningless dates. A cranium that had been reliably dated however, is NMB 1342 (also designated MR 1) from Layer D. This skull produced a date of 10 120 ± 200 BP (UCLA-1746A) (Protsch and Oberholzer 1975). Morphologically, it displays traits similar to UCT 378 from Elands Bay Cave. Although it resembles later Khoesan populations in overall morphology, it is large and robust. The face is small and flat and the frontal rises steeply (Louw 1960). The supraorbital region is also well developed. Protsch and Oberholzer (1975) have noted that the cranium is similar to Boskop in its large size and paedomorphic shape. These traits are apparent in other Layer D fossils too (Figure 4.4). Like UCT 378, the Layer D and C crania are large and robust, with pronounced supraorbital regions (Louw 1960; Braüer and Rösing 1989).

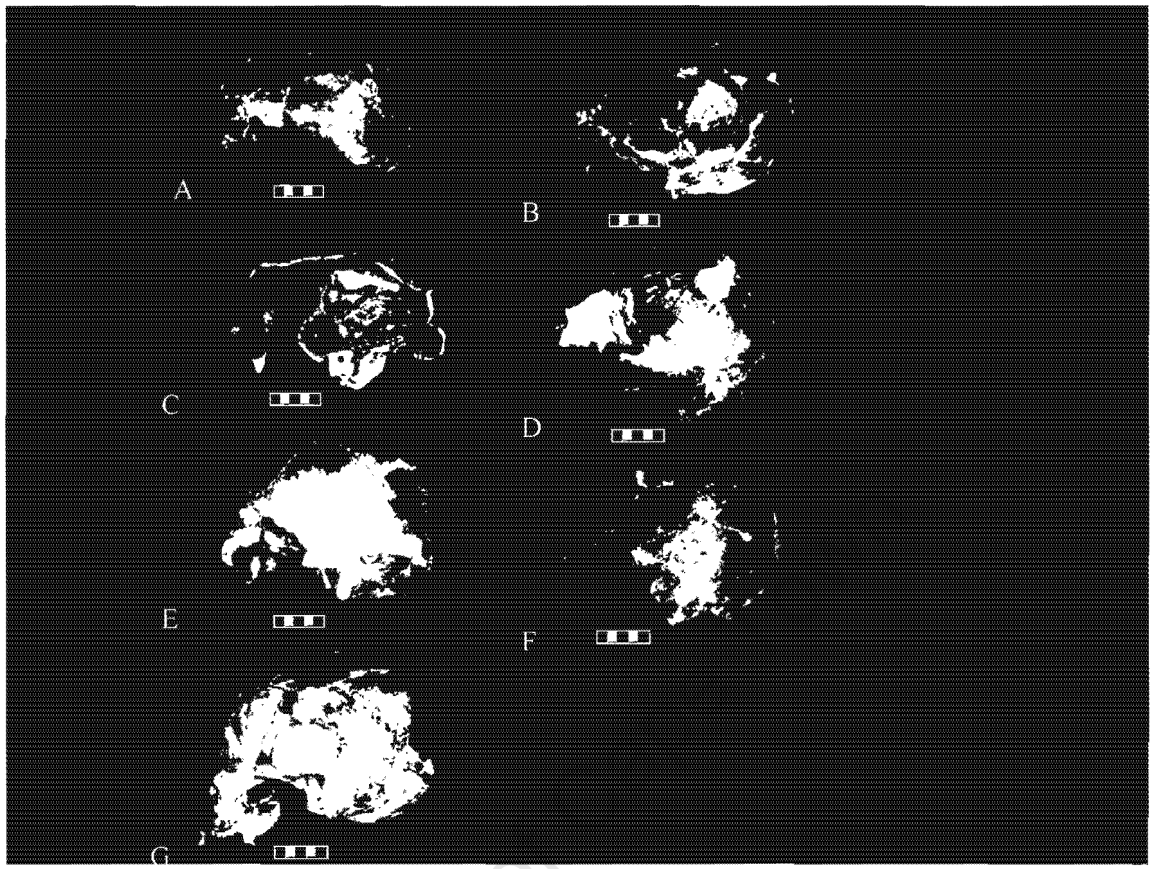

Figure 4.4: Lateral views of 7 fragmentary crania from Matjes River Rock Shelter. The 6 numbered crania are from the early to mid-Holocene levels. The single unmarked individual (G) is from unknown context, but is presented to demonstrate its marked supraorbital region.
A) MR 1-1
B) NMB 1279-1
C) NMB 1285-1
D) NMB 1295
E) NMB 1602-1
F) NMB-MR5
G) Unmarked individual.

WILTON LARGE ROCK SHELTER

Wilton Large Rock Shelter produced the cranial, mandible and some postcranial bones of a juvenile individual, ALB 119, which had been dated to 8260 ± 720 BP (GaK-1541) (Hewitt 1921; J. Deacon 1969, 1972; F. B. Silberbauer 1979). Braüer and Rösing (1989) have described the cranium as robust. It is pentagonal in shape with heavily developed frontal and parietal bosses. The frontal bone is steep and protruding. The superciliary

arches are not well developed and the face is low and flat. Despite being a sub-adult, this cranium resembles the crania from Elands Bay Cave and Layer D of Matjes River Cave in terms of combining a general Khoesan craniofacial morphology with overall large size and robusticity (Braüer and Rösing1989).

MID-HOLOCENE (*ca.* 7000 BP – 4000 BP)

Human skeletal material from the early part of the mid-Holocene is still relatively rare, but increases significantly towards the end of this period. Sites with significant numbers of early mid-Holocene human remains include a variety of locations in the Zuurberg Mountains in the Eastern Cape (FitzSimons 1923; Wells 1929; Rightmire 1978b), Matjes River Rock Shelter (Louw 1960; Protsch and Oberholzer 1975), Oakhurst (Drennan 1938; Goodwin 1938; Patrick 1989), Drury's Cave (Shrubsall 1922; Roux 1980; Sealy and Pfeiffer 2000) and Whitcher's Cave (FitzSimons 1926; Wells and Gear 1931; Schauder 1963; M. Turner 1970; Sealy and Pfeiffer 2000) in the southern region. Few human skeletons from South Africa's west coast date to the early mid-Holocene. However, when skeletons do occur, they are limited to the south-western region (A. G. Morris 1992 a, d). The limited information that is available on mid-Holocene craniofacial form suggests that many mid-Holocene crania still display the *large, robust morphology* of early Holocene populations.

MATJES RIVER ROCK SHELTER

Human skeletons from the early mid-Holocene at Matjes River Rock Shelter derive from Dreyer's Layer C. Meiring (1937) informally called Layer C the "Wilton Layer" and referred to the human skeletons from this layer as the "Wilton skeletons" (Meiring 1937).

To prevent confusion with the cultural material from Layer C, Louw (1960) later renamed the "Wilton skeletons" the "Keurbooms people". The layer D/C transition has been reliably dated to 7500 BP (Döckel 1998). Radiocarbon dates on human remains from Layer C indicate an age of between *ca.* 9500 BP and 7500 BP for this layer (Protsch and Oberholzer 1975), although as mentioned earlier, these dates are not very reliable.

Very little has been published on the mid-Holocene Matjes River material in the modern scientific era. The information that exists indicates that early mid-Holocene populations maintained the overall craniofacial morphology (low, broad faces and large neurocrania) and robusticity of early Holocene specimens (Louw 1960; Braüer and Rösing 1989).

OAKHURST CAVE

Goodwin's excavations in the 1930s at Oakhurst Cave produced 12 adult and 15 juvenile remains, many of which derive from mid-Holocene levels (Goodwin 1938; Oakley *et al.* 1977; Patrick 1989). Apart from Patrick's (1989) analysis which did not include an analysis of craniofacial variation, these skeletal remains have not been investigated biologically during recent times. Cranial analysis initially undertaken by Drennan (1938) indicate that the craniofacial morphology of the Oakhurst people were similar to the Matjes River Layer C crania. Drennan (1938) noted that both samples contained crania that were large and robust. This is to be expected since these cranial remains derive from contemporary periods at the two sites. The large, robust nature of the Oakhurst crania were later confirmed in studies by Rightmire (1970) and Hausman (1980).

LATE HOLOCENE (*ca.* 4000 BP – present)

The majority of the South African Holocene human skeletal sample dates to this period. This is not surprising, since human population numbers increased dramatically after *ca.* 4000 BP and the interment of the dead was commonly practiced (J. Deacon 1984b; Inskeep 1986; Hall and Binneman 1987; Hall 2000). The presence of largely temperate climatic conditions across much of the country also opened up new regions to human occupation. This is reflected in the human skeletal record. Although most late Holocene human skeletons still derive from the coastal regions, skeletons from the interior of the country were now more common than before. The Late Holocene is important in the context of this study because it is the period when livestock herding and farming were introduced to South Africa (after *ca.* 2000 BP). This has implications for population continuity in the region.

LATE HOLOCENE CRANIAL MORPHOLOGY

Our knowledge of human cranial morphology during the South African late Holocene is mainly derived from solitary open air burials in the dune landscape of the western and south-western regions, and cave burials in the southern region and in the Fold Belt Mountains. Despite the number of late Holocene skeletons available, there has never been any systematic analysis of dated crania from this period. Research focussing on temporally stratified samples of postcranial skeletal material is suggestive of biological changes having occurred during this period though. In the southern region, Sealy and Pfeiffer (2000) highlighted a period of decline in mean body size between 3300 BP and 2000 BP, including some very short adult statures, particularly in women. Recently, on

the basis of a larger, better dated sample, Pfeiffer and Sealy (2006) determined that the period when statures were at a minimum occurred slightly earlier, between *ca.* 4000 and 3000 BP. They hypothesised that widespread growth problems at the time were responsible for these reductions in stature.

Although it is not known to what extent the reduction in body size affected cranial form, descriptions of cranial morphology for the period 4000 to 2000 BP indicate that these populations fell well within the range of variation of recent gracile Khoesan populations both in terms of size and shape. Jerardino *et al.* (1992) describe the cranium of a male *ca.* 2700 BP skeleton discovered on the Northern Cape coast as having a flattened face, low upper facial height, anteriorly prominent zygomatic bones, a wide nasal bridge and a forehead that is wide and bossed. The shape of the skull in *norma verticalis* is pentagonal. A.G. Morris and colleagues (Inskeep 1987) compared the crania of Nelson Bay Cave human skeletons from the late Holocene to modern comparative skeletal samples of Caucasoid, Negroid and Khoesan people. All crania fell very close to the Khoesan population centroid. At the site of Byneskranskop, de Villiers and Wilson (1982) analysed the crania of three individuals that dated from the late Holocene. These authors note that the crania resemble recent gracile Kalahari San populations. A. G. Morris *et al.* (1987) described the cranium of a male *ca.* 2400 BP skeleton discovered at Snuifklip in the southern region as falling within the range of variation of recent Khoesan populations. The moderate development of the glabellar prominence and superciliary eminences indicate that this individual was quite gracile (A. G. Morris *et al.* 1987).

Two recent studies performed on dated postcranial remains primarily from the Cape coastal regions, indicate that post-2000 BP populations were significantly taller than pre-2000 BP people (P. Smith *et al.* 1992; Wilson and Lundy 1994). Gene flow from immigrant herders into the region was suggested as the most likely reason for an increase in overall stature after 2000 BP (P. Smith *et al.* 1992). These results supported colonial reports that historic herders were taller than hunter-gatherers. Cranial evidence apparently supported the post-cranial evidence for gene flow. Some authors have found that the cranial dimensions of recent Khoekhoe pastoralists are larger and more robust than those of recent San hunter-gatherers (Stern and Singer 1967; Rightmire 1970). As mentioned earlier, a study by Hausman (1980) indicated that post-2000 BP crania in the South African interior differed from pre-2000 BP populations in the Fynbos Biome in terms of an increase in neurocranial height and greater overall cranial size. In contrast, she found no significant cranial differences when she compared populations that occupied the Fynbos Biome. Hausman (1980) interpreted the craniofacial changes she observed in the interior as evidence that the greatest morphological variation occurred in the northern interior of the country, at the point of the introduction of pastoralism.

The genetic status of post-2000 BP Khoesan populations is however not as clear as much of the above evidence appears to suggest. As discussed in Chapter 3, the results of previous studies of Khoesan craniofacial variation are unreliable because of methodological problems. The increase in stature and cranial size in late Holocene populations can be explained by factors other than the migration of genetically distinct herders. For instance, Pfeiffer and Sealy's (2006) comprehensive study of post-cranial

change during the Holocene demonstrates that stature levels actually began to recover at *ca.* 3000 BP and not 2000 BP as suggested by the earlier studies by P. Smith *et al.* (1992) and Wilson and Lundy (1994). They ascribe this recovery to hunter-gatherers successfully adapting their socio-economic behaviour to cope with food security problems. That they did not observe a dramatic change in stature levels at 2000 BP is consistent with a hypothesis of genetic continuity before and after 2000 BP (Marks 1972; Schrire 1980, 1992; Schrire and J. Deacon 1989). Similarly, the presence of larger crania during the last 2000 years may be linked to a general increase in body size at 3000 BP.

There is currently no secure evidence that San and Khoekhoe were biologically distinct from one another. The only time that we can say with confidence that local hunter-gatherers came into contact with immigrants, was with Negroid farmers in the interior and on the south-east coast of South Africa. The issue of whether genetically distinct pastoralists immigrated into the Fynbos Biome thus remains largely unresolved.

SUMMARY

The earliest fossil evidence for Khoesan-like craniofacial morphology is the terminal Pleistocene Fish Hoek cranium (Howells 1969; Rightmire 1974, 1978b). Prior to this, South African human populations displayed a generalised African morphology (A. G. Morris 1992b). The limited cranial evidence that is available for study suggests that early to mid-Holocene human populations resembled recent Khoesan groups like the Kalahari San in terms of facial morphology, but were relatively larger and more robust (Braüer and Rösing 1989; A. G. Morris 1992a). This needs to be tested with a larger sample.

Braüer and Rösing (1989) have suggested that cranial robusticity decreased during the Holocene. Evidence from the early part of the late Holocene appears to support this contention. It was between *ca.* 4000 BP and 3000 BP that populations in the Cape Biome displayed widespread decreases in stature levels. Pfeiffer and Sealy (2006) have attributed this phenomenon to widespread growth problems experienced by populations struggling to come to terms with increased population densities and resulting pressures on scarce resources. Although there has never been a systematic study to determine whether there was a concurrent decrease in cranial size and robusticity levels at this time, individual finds dating to the late Holocene display gracile cranial morphology similar to that of recent Kalahari San populations. Based on this evidence it is tempting to argue that modern Khoesan cranial morphology emerged during the late Holocene, and that early to mid-Holocene populations, although Khoesan-like, were sufficiently large and robust to fall outside the range of craniofacial variation of recent populations.

Contrary to the suggestions of Braüer and Rösing (1989), stature levels started to recover at *ca.* 3000 BP, a millennium prior to the introduction of herding to the research area. Statures eventually recovered to pre-4000 BP levels during the last 2000 years. Pfeiffer and Sealy (2006) have suggested that the initial recovery was related to hunter-gatherers adapting their subsistence strategies to cope with existing food shortages. If the increase in stature was related to a general recovery in the health status of indigenous populations to pre-4000 BP levels and not to external factors such as gene flow, one might expect a similar recovery in cranial size and robusticity levels. It is possible that this may explain the presence of some large, robust crania in the post-2000 BP Khoesan skeletal record

and not gene flow from biologically distinct herders. The next chapter describes the South African LSA archaeological record.

CHAPTER FIVE

THE SOUTH AFRICAN LATER STONE AGE ARCHAEOLOGICAL RECORD

INTRODUCTION

Even though the start of the LSA in southern Africa dates back to at least 20 000 years ago, significant similarities in the belief systems and material culture of LSA people and those of ethnographically documented Kalahari San only began to emerge during the Holocene (J. Deacon 1984b). The mid-Holocene in particular represents an interesting period in South African prehistory. It is at this time that sites in the eastern region and southern region display an elaboration of material culture and burials (J. Deacon 1984b; Hall 1990). Shortly afterwards, there is a significant move in the direction of intensified resource exploitation and land use. These changes have been best documented in the Cape Ecozone and the Thukela Basin in KwaZulu-Natal (Binneman 1996, Hall 1990, Mazel 1989). After *ca.* 2000 BP, herding and farming entered South Africa, adding to the complexity in social and economic relations. In other regions of the world, these factors have led to significant alterations in the biology of populations. This chapter reviews our knowledge of the South African LSA record. Emphasis is placed on the evidence for environmental, cultural, subsistence and demographic change during the Holocene. Although the western, south-western, southern and south-eastern coasts and adjacent coastal forelands of South Africa are the focus of this thesis, archaeological changes within these regions are discussed within the context of the broader South

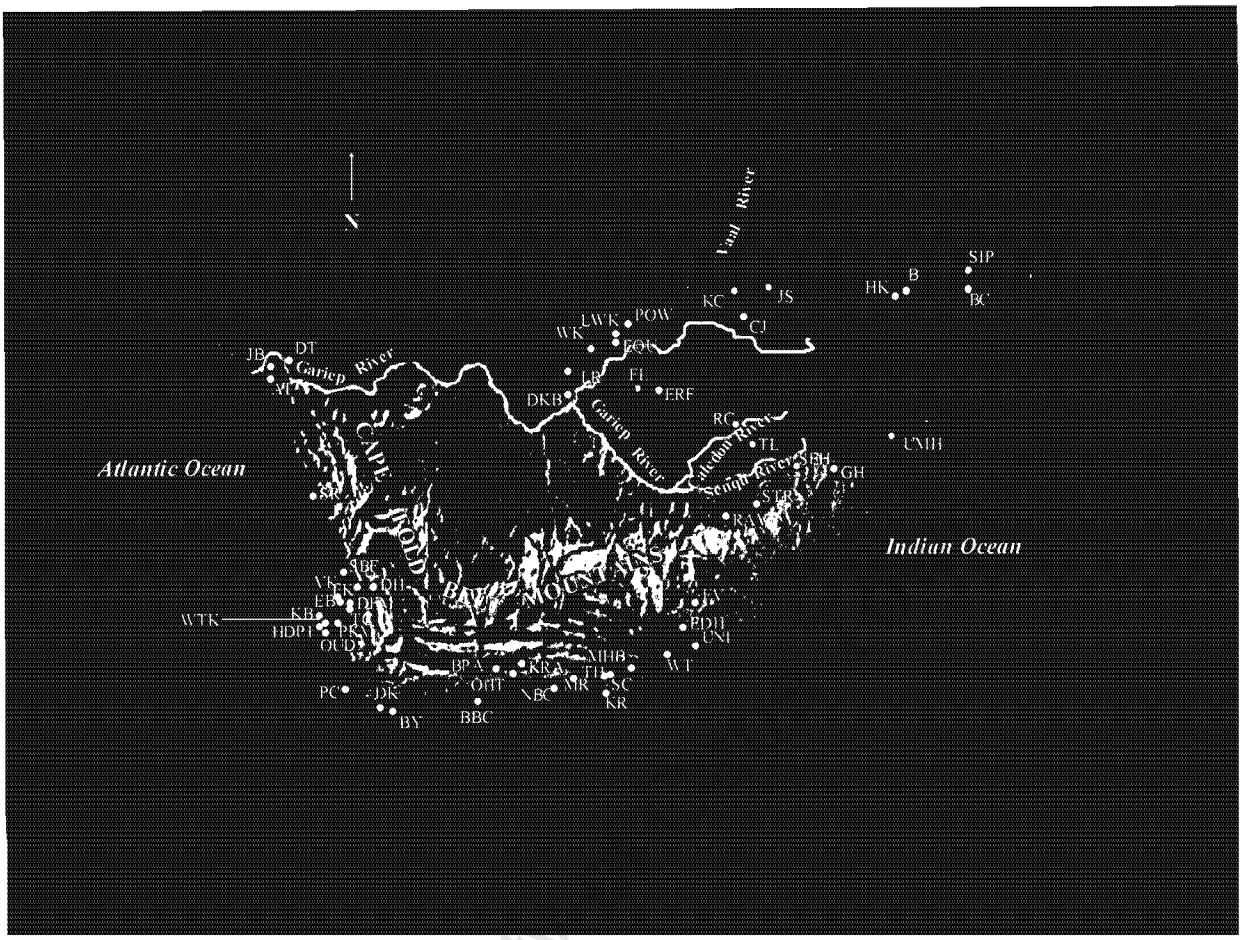

Figure 5.1: The locations of the archaeological sites discussed in this thesis.
AT: /Ai tomas **B**: Bushman Rock Shelter **BBC:** Blombos Cave **BC**: Border Cave **BPA**: Boomplaas **BY**: Byneskranskop **CJ**: Cave James **DFM**: Dune Field Midden **DH**: De Hangen **DK**: Die Kelders **DKB**: Dikbosch **DT**: Die Toon **EB**: Elands Bay Cave **EDH**: Edgehill **ERF**: Erfkroon **FK**: Faraoskop **FL**: Florisbad **FV**: Fairview **HDP 1**: Hoedjiespunt 1 **HK**: Heuningneskrans **JB**: Jakkalsberg **JS**: Jubilee Shelter **KB**: Kasteelberg **KC**: Kruger Cave **KRA**: Kangkara **KR**: Klasies River **LWK**: Little Witkrans **LR**: Limerock **MHB**: Melkhoutboom **MR**: Matjes River Rock Shelter **NBC**: Nelson Bay Cave **OHT**: Oakhurst Cave **OUD**: Oudepost **PC**: Peer's Cave **PKM**: Pancho's Kitchen Midden **POW**: Powerhouse Cave **RAV**: Ravenscraig **RC**: Rose Cottage Cave **SBF**: Steenbokfontein **SC**: Scott's Cave **SEH**: Sehonhong **SIP**: Siphiso **SR**: Spoegrivier **STR**: Strathalan Cave **TC**: Tortoise Cave **TH**: The Havens Cave **TL**: Tloutle **UNI**: Uniondale **UMH**: Umhlatuzana **VK**: Vensterklipkop **WK**: Wonderwerk Cave **WT**: Wilton Large Rock Shelter **WTK**: Witklip

African archaeological record. In this way, this chapter will provide a framework within which the biological influences of environmental and cultural change on Holocene

human populations can be examined. The locations of the archaeological sites mentioned in the text are illustrated in Figure 5.1.

INTRODUCTION TO THE SOUTHERN AFRICAN LATER STONE AGE

The latter part of the LSA was a relatively dynamic time in southern African prehistory. It was particularly during the last 10 000 years, or the Holocene, that the LSA became characterised by a number of innovations, including an explosion in rock art, deliberate burial of the dead, the use of bows and arrows, the appearance of bored digging-stick weights, the increased frequency of bone tools, tortoise-shell bowls and within the last 2000 years, the appearance of earthenware pottery (J. Deacon 1984b). Throughout this time, there were a number of changes in the style and composition of stone tool assemblages, as well as in indicators of subsistence strategies.

The advent of the LSA has for some time been a point of contention amongst archaeologists. Beaumont *et al.* (1978) argued that the MSA/LSA transition at Border Cave lay between 40 000 and 60 000 years ago. This date is, however, not universally accepted. Assemblages in the *ca.* 50 000 to 20 000 time range are notoriously unstandardised, are difficult to characterise, and vary markedly between regions. For instance, the Early Later Stone Age (ELSA) assemblage (Beaumont and Vogel 1972) identified by Beaumont *et al.* (1978) at Border Cave is absent at the inland site of Rose Cottage Cave (Wadley 1997). Instead, Rose Cottage has a transitional assemblage which includes both MSA and LSA features. This is sandwiched between clearly MSA and LSA assemblages. Readily characterisable LSA assemblages make their appearance only after

Stone Tool Industry	Date	Lithic Technology	Primary raw Material	Non-lithic artefacts	Subsistence Activities
Robberg Industry	*ca.* 21 000 BP - *ca.* 12 000 BP. At some interior sites late variants occur until *ca.* 9500 BP.	Microlithic industry. Bladelet rich.	Fine grained material such as crypto-crystalline silicas, quartz and opalines dominate.	Wide range of non-lithic tools, but are less numerous than in later periods. Artefacts include: ostrich eggshell beads, ostrich eggshell water containers, tortoise shell bowls, bone beads, bone spatulae, bone points, bone fish gorges, ochre, decorated ostrich eggshell, perforated marine shell and decorated tortoise shell.	Concentration on large migrant ungulates. Fewer small game species present. Marine foods and plant foods are rare.
Oakhurst Complex: 4 Geographic variants occur: Albany in Cape Fold Belt and forelands; Kuruman in Northern Cape; Lockshoek in Karoo and Free State; Pomongwan in Matopo Hills.	*ca.* 12 000 BP - *ca.* 8 000 BP. Some late occurrences at ca. 7000 BP.	Primarily macrolithic industry. Bladelets and bladelet cores are rare; large flakes and scrapers are common.	Coarse grained material such as Quartzite and hornfels dominate.	Increase in non-lithic artefact manufacture. These include: ostrich egg-shell beads, ostrich eggshell pendants, decorated ostrich eggshell water containers, tortoise shell pendants and bowls, perforated marine shell and a variety of bone tools.	Reduced occurrence of large migrant species. Increased concentration on non-gregarious small ungulates. Increased exploitation of small game such as hyrax and dune molerat. Increased presence of marine foods. Increased occurrence of fruiting plant species.
Wilton Complex: Classic Wilton	*ca.* 7000 BP - *ca.* 4000 BP.	Increase in formal tool manufacture. Microlithic industry. High number of segments present.	Fine grained material such as quartz, opalines, silcrete dominate.	Further increase in non-lithic artefact manufacture. Artefacts include: various ornaments and water containers made from ostrich egg shell, marine shell pendants, tortoise shell pendants and containers, various bone tools, rope made out of plant material and animal hide.	Concentration on small and medium non-gregarious ungulates, increased exploitation of ground game such as tortoise and dune molerat, increased plant exploitation particularly of geophytes, increased marine food exploitation.
Post -Classic Wilton	*ca.* 4000 BP -	Increase in backed	In addition to the	Same as above, with	Same as above

Table continued :

	colonial period.	bladelets, points, and adzes in certain regions. Some coastal assemblages possess large unretouched flakes and flaked cobbles.	use of fine grained material, informal tools were also manufactured on coarse grained material such as quartzite.	the addition of pottery at ca. 2000 BP.	but with the addition of domesticates after *ca.* 2000 BP.

Table 5.1: The characteristics of the three main subdivisions of the South African LSA.

ca. 20 000 BP (Mitchell 2002). This is the period that will be covered in this review. The discussion follows the conventional subdivision of the LSA into stages defined on the basis of major changes in the stone artefact sequence as outlined in H. J. Deacon (1976) and J. Deacon (1984a, b). Within this scheme, cognisance is taken of major changes in subsistence. Thus, along with changes in the stone artefact record, the introduction of herding and farming are identified as pivotal stages during the LSA. The characteristics that exemplify each of these stages are summarised in Table 5.1.

EARLY INTERPRETATIONS OF THE SOUTHERN AFRICAN LSA SEQUENCE

In the first major synthesis of the southern African Stone Age sequence, two parallel technological traditions were recognised: (1) the *Smithfield*, a largely macrolithic tradition that occurred in the inland areas of South Africa; and (2) the *Wilton*, a microlithic tradition that occurred mainly in the coastal regions of southern Africa (Hewitt 1921; Goodwin and Van Riet Lowe 1929). While the Smithfield was viewed as a locally developed industry, the microlithic Wilton was attributed to immigrant populations (Goodwin and Van Riet Lowe 1929). This hypothesis was primarily grounded in the many similarities between the Wilton and microlithic assemblages from further north in the continent. It was also based on a widely held perception that all

human populations possessed unique modes of material culture which differentiated them from other populations. In this way, material culture became linked to ethnicity. Inevitably, similarities in material culture between different geographic regions gave rise to theories of migration (Goodwin and Van Riet Lowe 1929).

In seeking the source of local cultural variation outside the borders of southern Africa, early archaeologists mirrored the practice of early physical anthropologists, who themselves had widely attributed the source of local craniofacial variation to the influx of immigrant populations (e.g. Meiring 1937). Taken together then, the cultural and biological data appeared to complement each other quite nicely. The microlithic component of the South African LSA was thought to have accompanied several migratory waves of anatomically modern human populations, on their southward migration into southern Africa. These people and their material culture would eventually come to replace residual South African MSA inhabitants both culturally and biologically, giving rise to the Bushmen (Goodwin and Van Riet Lowe 1929; Meiring 1937).

According to J. Deacon (1984a, b), descriptions of these two industries were almost exclusively qualitative prior to the 1970's. Hewitt (1921) noted that the material at Wilton Large Rock Shelter, the Wilton type site in the eastern region, was essentially homogenous. Wilton assemblages were said to contain high frequencies of microlithic tools, particularly small convex scrapers and backed pieces, made from various fine grained raw materials. The presence of backed 'crescents' was thought to be a distinctive marker of Wilton assemblages (Goodwin and Van Riet Lowe 1929). In contrast to the

Wilton, the Smithfield industry was limited mainly to open locations in the South African interior. Van Riet Lowe, who worked as a civil engineer, had the opportunity to analyse many Smithfield occurrences during road construction activities. He identified three types of Smithfield assemblages which he thought represented early, middle and late phases in a developmental sequence. J. Deacon (1984a, b) notes that despite lacking any stratigraphic context in these open occurrences, Van Riet Lowe nevertheless divided the Smithfield into A, B and C assemblages respectively. Smithfield A assemblages, hypothesised to be the oldest in the sequence, came from open sites, were almost exclusively manufactured out of hornfels, and were often heavily patinated. Tools were generally large and robust, and consisted primarily of side struck flakes and large D-shaped scrapers. Smithfield B assemblages, of intermediate age between A and C assemblages, also occurred mostly in open sites. However, tools were generally smaller than those from Smithfield A assemblages. Hornfels was again the preferred raw material, but tools were unpatinated, suggesting a younger age than the Smithfield A. End-of-blade scrapers, also informally known as "duckbilled" scrapers, were particularly evident in B assemblages, along with perforated stones, grindstones and ceramics. In contrast to the two earlier types, Smithfield C assemblages were microlithic and primarily associated with rock shelters in the eastern Free State. Agate, chalcedony and chert, as opposed to hornfels, were the preferred raw materials. Van Riet Lowe was struck by the tendency of the Smithfield to become more like the Wilton as the sequence progressed from A to C assemblages. He attributed this to the cultural influence of new migrants on the indigenous manufacturers of the Smithfield (J. Deacon 1984a, b; Goodwin and Van Riet Lowe 1929).

THE DAWN OF THE MODERN INTERPRETIVE FRAMEWORK

According to J. Deacon (1984a, b), the scheme proposed by Goodwin and Van Riet Lowe (1929) dominated archaeological research until the next major synthesis was proposed by J. D. Clark (1959). Existing observations on the nature of occurrences were extended in this synthesis. Nevertheless, the basis of the migratory theory for explaining variability in the archaeological record remained. A major breakthrough in the interpretation of archaeological assemblages occurred in the 1960s, when researchers realised just how deficient past qualitative descriptions and non-standardised typologies had been when it came to investigating variability in archaeological assemblages (J. D. Clark *et al.* 1966; Inskeep 1967). During the course of subsequent research, there was a concerted effort to establish a standard typology whereby LSA assemblages could be described (H. J. Deacon 1969, 1972; Sampson 1967a, b, 1972, 1974). According to J. Deacon (1984a), archaeologists also recognised a need to improve the use of cultural terminology at the Burg Wartenstein conference on African prehistory in 1965. To try to halt the erosion of the meaning of cultural terminology, a hierarchical set of terms were proposed. Archaeological occurrences were grouped into *phases*. Phases, in turn, were grouped into *industries*, which in turn were grouped into *industrial complexes*. However well-intended the process of term standardisation was, Parkington (1984a) notes that the actual terms were themselves not well defined, leading to further misuse and confusion. In addition, the continued association between artefact assemblage and ethnicity remained (Mitchell 1988).

J. Deacon (1984a) notes that within the milieu of a greater emphasis on more structured research designs and improvements in radiocarbon dating techniques, archaeologists began to review early technological descriptions and classification schemes. Working primarily with coastal and near coastal assemblages in the eastern and southern regions, H. J. Deacon and J. Deacon started constructing a complex picture of temporally related changes in the LSA along these sections of South Africa's coast. One of the first tasks which these two researchers undertook was a re-evaluation of the Wilton sequence. In 1966/1967, they re-excavated Wilton Large Rock Shelter. The research methodology was designed to investigate changes in both stone tool function and style (J. Deacon 1969, 1972). Contrary to Hewitt's (1921) description of the stone tool assemblage from Wilton Large Rock Shelter, J. Deacon (1969, 1972) found that the assemblage displayed significant levels of heterogeneity across time, both in terms of relative frequencies of formal tools and changes in the style of tools. These changes, J. Deacon (1969, 1972) argued, were more in keeping with the ontogenetic development of a single cultural system, than the result of external cultural influences. Similar patterns of heterogeneity were also evident in Wilton assemblages from sites such as Boomplaas Cave and others (H. J. Deacon 1969, 1976; H. J. Deacon and J. Deacon 1963; J. Deacon 1972, 1974). The realisation that the temporal variation displayed by the Wilton was more in keeping with the birth, life and death of a cultural system, placed the long established migratory theory in serious doubt.

Goodwin and Van Riet Lowe's (1929) scheme was further eroded when J. Deacon (1974) undertook a temporal and geographical analysis of a series of South African LSA

radiocarbon dates. In this analysis, she was able to show that the Smithfield A, B, and C, as described by Van Riet Lowe (Goodwin and Van Riet Lowe 1929), hardly represented the developmental sequence of a single cultural system. Instead, she found that there was a discontinuity in occupation in the South African interior, particularly in the Karoo, between about 8000 and 4000 BP. This she ascribed to the existence of unfavourably dry climatic conditions during the early-mid-Holocene. Since the mid-Holocene was the time of the Wilton, the absence of people in the interior explains the absence of the Wilton. Further, she found that there were no dates from the early to mid-Holocene that could be ascribed to the Smithfield. Dates for the Smithfield fell either in the ninth to thirteenth millennia, or after the fifth millennium before present. Based on these observations, J. Deacon (1974) rejected the existence of two co-existing LSA traditions, the Smithfield and the Wilton. Instead, she proposed that the Wilton and the Smithfield were part of a single evolving South African LSA tool making tradition, and that variability in the sequence was primarily due to temporal changes and geographic differences in human occupation (J. Deacon 1974).

At the same time that the Deacons were re-evaluating the South African stone tool sequence, Garth Sampson set up a similar research project. Working mainly in the interior of the country, Sampson's (1967a, b, 1972) primary aim was to date the Smithfield. In an attempt at implementing the terminology proposed by the Burg Wartenstein Conference, he proposed three successive industrial complexes and a possible fourth for the South African LSA. Within each industrial complex, he recognised various regional industries and their sub-divisions. In the Sampson (1974) scheme, the

oldest industrial complex, dubbed the Oakhurst complex, was broadly equivalent to Goodwin and Van Riet Lowe's (1929) Smithfield A. Dated to between *ca.* 12 000 BP and *ca.* 8000 BP, the Oakhurst complex had two regional variants: the Lockshoek industry in the Karoo and Free State, and the Pomongwan in Botswana and Zimbabwe. Sampson's (1974) second industrial complex was the mid-Holocene Wilton. Two variants were recognised, namely the Coastal Wilton and the Interior Wilton. Although diverse, both variants of the Wilton were said to have passed through early, classic, developed and ceramic phases respectively (Sampson 1974), supporting J. Deacon's (1969, 1972) findings. The Smithfield constituted Sampson's (1974) third industrial complex. It included Van Riet Lowe's B and C assemblages. In the interior, the Smithfield was said to postdate the Wilton, while along the coast, it was said to have been contemporary with the end of the Wilton or *Strandloper* sites. The *Strandloper* sites constituted a possible fourth industrial complex within Sampson's (1974) scheme. This term relates to late open coastal assemblages, particularly those in the south-western region's dune landscapes, which contained a combination of unstandardised tools and pottery. Parkington (1984a) notes however that the *Strandloper* category may not have had sufficient cohesion to qualify as an industrial complex. Within the Sampson (1974) scheme, changes in stone tool assemblages were either driven by migration/diffusion or by changes in the environment. Much like Goodwin and Van Riet Lowe (1929), Sampson (1974) focussed on particular artefact types, often relating their introduction to contact between immigrants and locals.

The Deacon model of a single evolving stone tool making tradition was further developed with results from excavations at Melkhoutboom in the eastern region and Nelson Bay Cave in the southern region (H. J. Deacon 1969, 1976; J. Deacon 1984a; Klein 1972a, b, 1974). Both sites have deep sequences which produced Late Pleistocene LSA stone tool assemblages that pre-dated Sampson's (1974) Oakhurst Complex. Not only did these sites provide evidence that the LSA was already present in the region well before the start of the Holocene, but well-preserved faunal and floral records provided a unique opportunity to investigate changes in hunting and subsistence activities during the LSA. Studies investigating temporal changes in faunal and plant remains were carried out in parallel with studies on stone artefact sequences (H. J. Deacon 1972, 1976, 1979; Klein 1972a, b, 1974, 1976, 1977). Significantly, these studies were able to demonstrate that shifts in artefact frequencies and styles co-varied broadly with changes in subsistence patterns, as reflected by the faunal and floral remains. This discovery suggested that variation in stone tool assemblages may be linked to changes in adaptive strategies on the part of prehistoric people (H. J. Deacon 1976). For instance, the newly discovered late Pleistocene LSA assemblage was associated with a unique range of faunal remains composed mainly of large, mobile grazing antelope, few small browsers and limited evidence of plant food exploitation. With the progression towards the later Wilton, the size and composition of animal species changed, while the exploitation of edible plants increased. Faunal and floral evidence from the Wilton levels suggested a subsistence strategy based on the gathering of plant foods and shellfish, supported by the snaring of small antelope and capture of tortoises and other small animals. Based on these new discoveries, H. J. Deacon (1976) presented his model of homeostatic plateaux, where the

LSA stone tool sequence in the southern and eastern regions was split into a new three-stage sequence: the Robberg (18 000 – 12 000 BP), Albany (12 000 – 8000 BP) and Wilton (8000 BP – colonial period) industries respectively (H. J. Deacon 1976). These three stages represented periods during which the adaptive response of people to their environment (as reflected in faunal and floral remains) was hypothesised to have been relatively stable, with shifts required at *ca.* 12 000 BP and *ca.* 8000 BP due to changes in environmental conditions. Within this scheme, the influence of successive waves of migrating populations on changing stone tool technologies was rejected. Instead H. J. Deacon (1976) proposed that tool making techniques diffused along linguistic pathways. Technologies were adjusted to cope with changes in climate and habitat through time and across space (H. J. Deacon 1976).

The Deacon model for explaining variability in the South African archaeological sequence was challenged by Parkington (1980). Basing his ideas primarily on observations of archaeological assemblages in the western and south-western regions, Parkington (1980) specifically questioned the existence of homeostatic plateaux in the archaeological record. Instead, he preferred a model of more continuous change where stone tool variation reflected changes in site use by people over time (Parkington 1980). Within this model, the role of "place", or in other words, the situation of the site in a particular landscape at a specific time in the past, is a key concept. The concept of "place" is defined as the set of opportunities that a location affords and thus the probability that particular activities will take place there (Parkington 1980). According to Parkington's (1980) argument, variability within the southern African stone tool

sequence was primarily related to activity differences between sites, rather than change through time. Where a specific tool appears to be "time-controlled", the reason may be more the result of differences in local resources than changing preferences in artefact manufacture. Thus Parkington (1984a) argued that open Oakhurst occurrences may simply be contemporary typological alternatives to cave site Robberg occurrences. The late occurrence of the Robberg Industry at certain sites such as Rose Cottage Cave (Wadley 1997) in the Free State Province may appear to support Parkington's (1984a) scheme, however, at other sites such as at Nelson Bay Cave and Boomplaas, the Robberg is replaced relatively early on by the Albany, the Cape Fold Belt variant of the Oakhurst, and never reappears (J. Deacon 1984a, b). In this sense, these industries do appear to be time-controlled.

THE MODERN INTERPRETIVE FRAMEWORK FOR THE SOUTH AFRICAN LSA

The general consensus view within the field today is that despite variability between sites, there are genuine wide ranging temporal changes in material culture, subsistence and demography through the Holocene. The contemporary subdivision of the southern African LSA stone tool sequence borrows extensively from the Deacon (H. J. Deacon 1976) and Sampson (Sampson 1974) models. The earliest industry within the modern scheme is the terminal Pleistocene Robberg Industry (*ca.* 22 000 – 12 000 BP) (H. J. Deacon 1976). The Robberg Industry is replaced by the Oakhurst Complex (*ca.* 12 000 – 8 000 BP) with its various geographic variants. The Oakhurst Complex in turn is replaced by the Wilton Complex (Sampson 1974) at *ca.* 8000 BP. The Wilton Complex is characterised by an early phase (*ca.* 8000 - 7000 BP), a classic phase (*ca.* 7000 – 4000

BP), and a post classic phase (4000 – colonial times) which includes the addition of pottery after *ca.* 2000 BP (J. Deacon 1972; Sampson 1974). Each of these periods will be discussed in more detail below.

THE LATE PLEISTOCENE TO EARLY HOLOCENE:

THE ROBBERG INDUSTRY

The Robberg Industry, also known in the past as "Late Pleistocene microlithic assemblages" (J. Deacon 1984b) or "early microlithic assemblages of southern Africa" (Mitchell 1988), represents the first widely occurring LSA technology in southern Africa. Wadley (1996a) notes that the Robberg Industry was first recognised in the 1940's by the French archaeologist, Abbé Breuil, at Rose Cottage Cave in the Eastern Free State. Breuil's discovery, however, was never published. Fellow excavator, Malan (1958) merely referred to it as "pre-Wilton". The Robberg was first properly described and then officially recognised on the Robberg Peninsula in the Nelson Bay Cave assemblage. This southern region site became the type site for the Robberg Industry (J. Deacon 1978).

As Breuil had observed, the Robberg Industry is overwhelmingly a bladelet rich industry. Usewear and traces of mastic on some specimens suggest that bladelets were probably hafted (Binneman 1997; Binneman and Mitchell 1997; Williamson 1997). The Robberg is characterised by unretouched bladelets (<25 mm) manufactured from unfaceted single-platform cores. The lack of retouch on Robberg bladelets sets the Robberg Industry apart from microlithic assemblages in the Holocene (J. Deacon 1978; J. Deacon 1984a). Despite the commonality of bladelets and/or evidence of bladelet manufacture (bladelet

cores) though, Robberg assemblages vary substantially in terms of age of occurrences, tool composition and raw material use. At Rose Cottage Cave where the Robberg Industry was first (unofficially) recognised, the sequence is not very deep, with the base of the oldest Robberg level dated to 13 360 ± 150 BP (Pta-5601) (Wadley 1996a). However, the Robberg persists much later at Rose Cottage than at other sites, with a latest date of 9560 ± 70 BP (Pta-7275) being recorded (Wadley 1997, 2000a). The earliest known occurrences of the Robberg Industry are at Boomplaas Cave in the eastern region (*ca.* 21 000 BP) (H. J. Deacon 1995) and Sehonghong in Lesotho (*ca.* 20 000 BP) (Mitchell 1995). Along with Nelson Bay Cave, these two sites also contain the longest known Robberg sequences. Apart from Boomplaas Cave and Nelson Bay Cave, other sites with Robberg assemblages that fall within the focus area of this thesis are: Melkhoutboom (15 400 ± 120 BP) (UW-233) (H. J. Deacon 1976) in the eastern region; Kangkara (12 550 ± 110 BP) (Pta-782) (J. Deacon 1984a; Mitchell 1988) and Byneskranskop (12 730 ± 185 BP) (I-7948) (Schweitzer and Wilson 1978; Mitchell 1988) in the southern region; and Elands Bay Cave (*ca.* 12 000 BP) (Parkington 1980, 1990) and Faraoskop (Manhire 1993) in the western region. Sites with Robberg assemblages that fall outside the focus area of this thesis include Equus Cave and Wonderwerk Cave in the Northern Cape Province interior (Beaumont and D. Morris 1990); Umhlatuzana in KwaZulu/Natal Province (Kaplan 1989); Siphiso in Swaziland (Barham 1989) and Heuningneskrans in Mpumalanga Province (Mitchell 1988, 1995). Interestingly, these sites are all caves or shelters. Open air occurrences appear to be rare. Wadley (1996a) nonetheless remarks on unpublished accounts of open-site Robberg-like tools in Swaziland, while Churchill *et al.* (2000) make mention of the presence of Robberg-like

bladelets at the open-air site of Erfkroon in the Free State. Interestingly, Sampson's (1985) extensive survey of the Seacow Valley in the Karoo was unable to uncover any open-air Robberg assemblages.

Raw materials used in the manufacture of tools vary greatly between sites. This however, is primarily due to the local geology of the areas in which sites occur. Tools are overwhelmingly made from local materials. Exotic materials are present, but to a much lesser extent. For instance, at Boomplaas Cave, quartz is freely available in the Cango Valley where the cave is situated. This is also the dominant raw material at the site. Other materials include crypto-crystalline silicas, hornfels, quartzite and silcrete. Of these, silcrete is the only non-local raw material, and must have been brought in from outside the immediate surroundings of the cave (H. J. Deacon *et al.* 1984). At Nelson Bay Cave and Kangkara, quartzite, which is plentiful in the general surroundings of both caves, is the dominant raw material (Mitchell 1988). At Elands Bay Cave, quartz, which is readily available near the site in veins in Table Mountain Sandstone, is the dominant raw material (Mitchell 1988). At the two inland sites of Rose Cottage Cave and Sehonghong, opalines, which are widely available in the general area around these two caves, are the predominant raw material in assemblages (Mitchell 1995; Wadley 1996a). Quartz is hardly ever used in these two assemblages. If raw material is used as an indication of group mobility then, one would have to conclude that groups were not very mobile during the Robberg, which goes against H. J. Deacon's (1972) hypothesis of the Robberg people being highly mobile hunters. However, this argument presupposes that sites containing Robberg material were home bases. The use of local raw material may simply

mean that people did not carry raw material long distances, preferring instead to use the material that was most widely available to them wherever they happened to find themselves in the landscape. It is, however, interesting to note that quartz, which tends to fracture and is more difficult to manipulate than opalines and silcretes, dominate some coastal assemblages. If people moved widely, or maintained extensive trade networks, one may suppose that a premium would be placed on desirable raw materials such as opalines, and that these would occur in greater quantities than they do along the coast. This argument again presupposes that movement would have been between coastal and inland areas.

Tool manufacturing activities also appear to have varied quite substantially between sites. For instance, although the Robberg is known as a bladelet-rich industry, bladelets are rare in some Robberg assemblages. The inland assemblages from Sehonghong and Rose Cottage Cave contain the greatest number of blades and bladelets of all known Robberg occurrences. Sites which are either on or close to the coast, such as Boomplaas (J. Deacon 1984a), Nelson Bay Cave (J. Deacon 1984a), Kangkara, Byneskranskop and Elands Bay Cave (Mitchell 1988) have relatively fewer bladelets. Interestingly, Byneskranskop (Mitchell 1988) and Kangkara (J. Deacon 1984a) contain a high percentage of bladelet cores. This indicates that blades were manufactured at these sites, but were used somewhere else. The sites of Sehonghong and Rose Cottage Cave also contain the greatest number of rare retouched tools (Mitchell 1995; Wadley 1996a). Backed tools are more common at Rose Cottage Cave than at any other site (Wadley 1996a). At this site and Sehonghong, backed bladelets predominate. If one discounts

possible sampling issues and compares proportions of tools directly between assemblages, the variability in Robberg tool assemblages suggest that cave sites may have been only one of the places where tools were manufactured. They thus cannot be regarded as a focus for tool manufacture.

The largest collection of non-lithic artefacts comes from Boomplaas Cave. These include ostrich eggshell beads, apertures of ostrich eggshell water containers, a tortoise shell bowl, bone beads, spatulae and bone points (J. Deacon 1984a). At the site of Nelson Bay Cave, possible bone arrow linkshafts and bone fish gorges were discovered (J. Deacon 1984a). Melkhoutboom preserves fragments of ochre and fragments of decorated ostrich eggshell (Mitchell 1988). At Elands Bay Cave, Pettigrew (1977) has recorded the presence of a perforated *Donax* shell as well as a decorated tortoise shell fragment. Though the range of non-lithic artefacts present in terminal Pleistocene assemblages appears to be relatively broad, the quantities within each category are generally significantly smaller in comparison to Holocene assemblages.

The earliest expressions of the Robberg Industry were manufactured at a time that is generally regarded as the coldest period in southern Africa during the last 125 000 years. Dubbed the Upper Pleniglacial (*ca.* 25 000 – 16 000 BP), estimates of temperature reduction during this period vary from 8 - 9.5°C (Talma *et al.* 1974) to 5 - 5.5°C (Vogel 1983; Heaton *et al.* 1986) compared with the present. Generally, conditions were also drier than those experienced at present. The South African interior, particularly the Karoo (Partridge and Dalbey 1986) and the southern Kalahari (Beaumont *et al.* 1984), was

exceedingly dry. Along the southern coast, deep sea cores have attested to cooler ocean temperatures at *ca.* 18 000 BP and the weakening of the Agulhas Current (Prell *et al.* 1979), both of which would have reduced orographic precipitation in this area (J. Deacon 1984b). It is estimated that a reduction in mean annual temperature of 6°C could have decreased the amount of precipitable water by 30 - 50% along this coast (Gates 1976; Mitchell 1988). The coldest, most arid conditions occurred at around 18 000 BP, during the Last Glacial Maximum (LGM) (J. Deacon and Lancaster 1988). During this time, a large area of land would have been exposed along South Africa's south coast, with an extended coastal plain of over 100 km at some places (van Andel 1989). The mountains of the Cape Fold Belt would then have been approximately 70 to 90 km inland. This would have provided the Robberg people with a vast stretch of land on which to survive. According to Butzer (1984), the western region experienced an increase in precipitation during this time, unlike other areas. His claim is based on the investigation of dunes resulting from the marine regression of the Upper Pleniglacial. Butzer (1984) identified three palaeosol horizons which he attributed to three subhumid climatic phases between 25 000 and 15 000 BP. Butzer's (1984) claims are however disputed by J. Deacon and Lancaster (1988), who argue that the palaeosols that alternate with the dunes in the western regions are not reliable evidence for higher rainfall at this time. At the site of Elands Bay Cave, though, charcoal analysis appears to support Butzer's (1984) claims for wetter conditions in this region, at least in the general vicinity of the cave (Klein 1984, 1986; Cartwright and Parkington 1997).

The late expressions of the Robberg Industry fall within the Late Glacial (*ca.* 16 000 BP – 10 000 BP). Evidence from across many regions suggests the onset of markedly wetter climatic conditions almost immediately after the LGM. In the South African interior, precipitation increased noticeably in areas such as the Gaap Escarpment (Butzer *et al.* 1978) and the Kalahari Desert (Lancaster 1979; H. J. Cooke 1980). J. Deacon and Lancaster (1988) note that evidence from Boomplaas Cave indicates that the period from 16 000 – 12 000 BP was the wettest period in the last 70 000 years in the southern region. This is particularly evident in the re-establishment of woodland plant species and a change in the composition of micromammals (H. J. Deacon *et al.* 1984). Dune molerat sizes at Elands Bay Cave suggest that the environment was relatively dry in the western region at this time (Klein 1984, 1986). When one considers the faunal record, the Late Glacial was characterised by a relatively rapid change in the composition of small animal species and plants. Larger animal species lagged behind, with major changes post-dating 12 000 BP, when a range of large grazers became extinct (Klein 1980, 1984b).

The sequence at Boomplaas cave provides one of the most complete faunal and floral records for the time. Besides signifying a cold, generally dry glacial climate, this assemblage also reflects unusually low species diversity in both plant and animal remains during the Upper Pleniglacial (J. Deacon 1984b). Faunal lists from this time are routinely dominated by large migrant grazers with relatively few small, solitary browsers present. This has resulted in early descriptions of terminal Pleistocene people as migratory big game hunters (H. J. Deacon 1972). Recent studies have tended to paint a more complicated picture of subsistence at this time. According to Mitchell (1988), there is

little or no evidence that southern African hunters had access to the bow and arrow prior to the Holocene. Hunting weapons would thus have been limited to unaided throwing or thrusting spears. Mitchell (1988) notes that hunting with these methods would have resulted in even lower success rates than those recorded ethnographically for San hunters (Lee 1979; G. B. Silberbauer 1981). Alternative methods of hunting such as the driving of herd animals off cliffs may also have been practiced (Klein 1981). Nonetheless, hunting as a primary subsistence strategy may have been too unreliable for group survival at the time (Mitchell 1988).

In the absence of hunting as a main subsistence strategy, the exploitation of more reliable food sources such as plant foods, ground game (rock hyrax and molerats), tortoises and shell fish becomes essential for group survival. At Byneskranskop, tortoise and shellfish remains are present (Schweitzer and Wilson 1982). However, quantities are much lower than in later Holocene levels. This is particularly evident in the case of shellfish remains, which is probably a reflection of the site having been situated further inland relative to the terminal Pleistocene sea-level than was the case after 10 000 BP (Mitchell 1988). At Elands Bay Cave, substantial ground game remains are present, along with those of tortoises and small sedentary antelope. Together with the larger eland, these species represent the most common species in the terminal Pleistocene assemblage (Parkington 1977). The evidence for the exploitation of coastal resources at this site is scarce at this time. This is in all likelihood due to Elands Bay Cave being situated approximately 30km inland at and immediately after the LGM. Evidence for the utilisation of plants as a source of food is extremely rare in terminal Pleistocene assemblages in general.

Beaumont (1978) recorded the presence of edible seeds and leaves at Border Cave, while carbonised plant remains at Elands Bay Cave and Boomplaas hint at the possible exploitation of edible plants at this time (H. J. Deacon and Brooker 1976; J. Deacon 1984b). Despite this, it is true that terminal Pleistocene sites do not preserve evidence of the extensive geophyte exploitation evident during the Holocene.

The inclusion of a greater number of big game animals in the diets of terminal Pleistocene people in comparison to Holocene people probably has partly to do with the greater availability of these species. It has been hypothesised that the cold, dry glacial climates encouraged the spread of grasslands and thus the proliferation of large grazers (Klein 1980, 1984b). With a greater number of large grazers on the landscape, terminal Pleistocene hunters no doubt encountered these species more often than Holocene hunters. This, coupled with the lack of human pressure on resources, probably encouraged people to go for large game instead of focussing on more intensive subsistence activities. The paucity of shellfish in Robberg assemblages may be explained by the rise in the global sea level after the LGM. There is no doubt that humans were exploiting shellfish resources along the Cape coast from as early as the Last Interglacial, some 125 000 years ago, as is evidenced at Klasies River (Singer and Wymer 1982) and Hoedjiespunt 1 (Stynder *et al.* 2001). Evidence for this exploitation would have been lost with the Post-Glacial rise in sea level. Robberg assemblages that now occur close to the ocean would, during glacial times, have been situated inland, particularly those in or near the Cape Fold Belt. The scarcity of plant residues in Robberg assemblages are harder to explain. However, preservational issues may come into play here. It is nevertheless true that

plants are rare at Boomplaas Cave, where there is excellent preservation of organic material in general (H. J. Deacon and Brooker 1976).

Compared to the Holocene, archaeological occupations dating to the Upper Pleniglacial are relatively scarce on the southern African subcontinent. Archaeological occurrences in the southern African interior are particularly rare. This scarcity has been presented as evidence for a major decline in human population size at this time (Parkington 1990; Mitchell 2002). There may however have been other factors involved in the low site visibility. One view suggests that coastal regions, particularly the southern region, were preferentially occupied because they experienced higher and more reliable rainfall (in spite of glacial conditions) than most of the interior (J. Deacon and Lancaster 1988; Mitchell 1988). In addition, the broken topography of the adjacent Cape Fold Belt may have encouraged settlement as these areas provided people with greater ecological diversity in which to forage than would the interior (J. Deacon 1984a; J. Deacon and Lancaster 1988). An alternative view suggests that the main population concentration during the terminal Pleistocene may in fact not have been in the Cape Fold Belt Mountains and adjacent escarpment, but somewhere else. Parkington (1984a) proposed that the Robberg assemblages and associated faunal remains in the Fold Belt may in fact represent "occasional, peripheral and perhaps atypical reflections of a system centred elsewhere, in the interior for example" (Parkington 1984a). If this was the case, the paucity of inland archaeological occurrences at this time may be linked to issues of preservation. It is true that the majority of Robberg assemblages occur in caves or rock shelters, both inland and along the coast. Caves and shelters in turn, are more common

along the coast than inland, which could account for the greater visibility of Robberg assemblages along the coast. This however, does not account for the paucity of Robberg stone tools in the interior, granted that these may be more difficult to recognise in the open than in caves. Nonetheless, the existence of extremely cold, dry climatic conditions militates against there having been intensive human occupation of the interior during the Upper Pleniglacial (J. Deacon and Lancaster 1988; Mitchell 1988). An alternative region of population concentration may have been the now submerged continental shelf (Parkington 1990; A. G. Morris 2002, 2003). A. G. Morris (2002, 2003) has hypothesised that the exposed continental shelf may have formed part of an enlarged coastal foreland where the Khoesan phenotype would have evolved during the terminal Pleistocene.

There is no doubt that taphonomic issues and the reduced visibility of open sites may have served to mask the existence of Robberg occurrences in the interior to a greater extent than at the coast. However, based on ecological considerations and past climatic conditions, it is more likely that coastal regions, particularly those that are now under water, may have held the main concentration of people during the Upper Pleniglacial. Mitchell (1988) notes that for much of the Late Glacial, site distribution remained largely restricted to those areas that were occupied during the Upper Pleniglacial. This may have remained so until saturation levels were reached along the coast. At this time, reoccupation of the now better-watered and increasingly productive interior would have commenced (Mitchell 1988). No doubt, the changing coastline, related to the melting of the continental ice-sheets, would also have significantly reduced the coastal forelands. This in turn would have resulted in a readjustment in demographic patterns in these areas

(J. Deacon 1984b; J. Deacon and Lancaster 1988; Mitchell 1988) by the end of the Pleistocene.

THE OAKHURST COMPLEX

By approximately 12 000 BP, the Robberg Industry was gradually replaced by the Oakhurst, a complex of non-microlithic industries around the country. Four geographic variants of the Oakhurst Complex are recognised today: the Albany Industry in the Cape Fold Mountain Belt and its forelands (J. Deacon 1984b); the Kuruman in the Northern Cape (Humphreys and Thackeray 1983); the Lockshoek in the Karoo and Free State (Sampson 1974); and the Pomongwan in Zimbabwe's Matopo Hills (N. J. Walker 1995).

The earliest Oakhurst occurrences are dated to *ca.* 12 000 BP, and occur at the sites of Bushman Rock Shelter (Plug 1981), Heuningneskrans (Beaumont 1981) and Wonderwerk Cave (Humphreys and Thackeray 1983) in the South African interior. The earliest occurrence of the Cape Fold Mountain Belt variant of the Oakhurst, the Albany, is dated to *ca.* 11 000 BP at the sites of Nelson Bay cave (J. Deacon 1984b; Inskeep 1987), Elands Bay Cave (Parkington 1980, 1992) and Matjes River Rock Shelter (Louw 1960; Vogel 1970). At other coastal sites such as Byneskranskop (Schweitzer and Wilson 1982), Boomplaas (H. J. Deacon 1979; J. Deacon 1984b) and Oakhurst Cave (Patrick 1989), the Albany appears at *ca.* 9000 BP. Interestingly, in South Africa's eastern interior, a late variant of the Robberg Industry occurred until *ca.* 9000 BP, whereas in the rest of South Africa, it had largely disappeared by *ca.* 12 000 BP. Wadley (2000a) reported that the Robberg survived relatively late at Rose Cottage Cave, dating to *ca.* 9560 BP. At Siphiso Cave in Swaziland, Robberg bladelets continue to be manufactured until

approximately 9500 BP (Barham 1989). Similar dates were obtained for the Robberg at Umhlatuzana in KwaZulu/Natal, however, rotational slippage of sediments may be a problem at this site (Kaplan 1990). When the Robberg was eventually replaced by the Oakhurst at these sites, its presence was relatively short-lived. By 8000 BP, the Oakhurst industry was replaced by the Wilton Complex at the majority of sites. Late occurrences of the Oakhurst are evident at *ca.* 7000 BP at Good Hope Shelter in KwaZulu/Natal (Cable *et al.* 1980) and Kruger Cave in the North West Province (Mason 1988).

The shift from the Robberg to the Oakhurst is characterised by significant shifts in stone tool assemblages. These involve: (1) changes in raw material usage; (2) changes in flaking methods; (3) changes in the lengths of flakes; (4) changes in the size and shape of formal tools, particularly in terms of an increase in mean length; and (5) the absence of entire artefact classes which had previously been common (J. Deacon 1984 a, b; Mitchell 1988).

With the replacement of the Robberg by the Oakhurst, there is a concurrent shift in the choice of raw materials away from the use of fine-grained raw materials towards coarser materials. In her analysis of the lithic assemblages from Boomplaas, Nelson Bay Cave and Kangara, J. Deacon (1984a) demonstrated that in levels dating between *ca.* 12 000 and 8000 BP, people tended to choose raw materials that would produce large flakes. These materials included quartzite and hornfels in the case of Nelson Bay Cave and Boomplaas, and silcrete and hornfels in the case of Kangara (J. Deacon 1984a). As mentioned earlier, the Robberg assemblage at Boomplaas is dominated by quartz, while

at Nelson Bay Cave and Kangara it is dominated by quartzite. At Rose Cottage Cave, where fine-grained opalines had dominated Robberg assemblages, the Oakhurst assemblages exhibit the lowest use of opalines for any time during the Holocene. Though opalines continued to be used, the use of tuffaceous rocks, sandstone and hornfels increased at this site (Wadley 2000a). Interestingly, Mitchell (1996) reports that the use of coarser materials at Sehonghong peaked at *ca.* 11 000 BP, when the Robberg Industry was still being manufactured. The Oakhurst only replaces the Robberg at Sehonghong at *ca.* 9000 BP (Mitchell 1996), reflecting a trend at other sites in the eastern interior of South Africa.

J. Deacon (1984a) notes that at the sites of Nelson Bay Cave, Boomplaas and Kangara, the flaking methods used between *ca.* 20 000 and 12 000 BP is characterised by a high incidence of bladelet cores. These are associated with bladelets of which only a small proportion are retouched. Flakes are short, narrow and quite bladelike. Chips also tend to be common. Between *ca.* 12 000 BP and 8000 BP, chips become rare. At the same time bladelets and bladelet cores are rare or absent. Untrimmed flakes are longer, wider, and less bladelike (J. Deacon 1984a). In contrast to these three coastal sites, Rose Cottage Cave contains few large flakes (Wadley 2000a). Wadley (2000a) reports that mean lengths and widths of blades and bladelets are remarkably small throughout the Oakhurst. This she attributes to the size of available rock nodules in the area (Wadley 2000a).

The Albany assemblages at Nelson Bay Cave, Boomplaas and Kangara have a smaller range of formal tools than the later Wilton (J. Deacon 1984a). At all three sites, scrapers

are the most common formal tool. At the end of the Pleistocene, the dominant scraper type was the large Smithfield-A type. These were replaced by elongated end scrapers and scrapers with steep-sided retouch or naturally steep sides. At Rose Cottage Cave, formal tools are also rare at this time, with scrapers being the most common type (Wadley 2000a). At this site, end scrapers also increase in number towards the end of the Oakhurst series. Adzes and spokeshaves are rare in the Rose Cottage Cave Oakhurst assemblage (Wadley 2000a).

There was a general and significant increase in the manufacture of non-lithic artefacts such as ostrich eggshell beads and bone and shell artefacts after *ca.* 12 000 BP. J. Deacon (1984a) notes that bone artefacts are present at Nelson Bay Cave and Boomplaas, but not at Kangara. At these sites, ostrich eggshell was used to manufacture beads, pendants and decorated water containers. Tortoise shell was used to manufacture pendants and bowls. Perforated marine shell beads are present at all three sites. This is particularly significant in the case of Boomplaas, which even today is approximately 80 km from the coast (J. Deacon 1984a). Marine shell ornaments are also present at Sehonghong Shelter in Lesotho (Mitchell 1996). The increased frequency of ostrich eggshell beads and marine shell ornaments in archaeological assemblages after 12 000 BP, has been interpreted by Wadley (1993) as possibly signalling the development of social relations and exchange networks. This may help to explain the presence of marine shell in sites that are situated far from the coast.

Climatically, the late Pleistocene/early Holocene transition was marked by the onset of the current interglacial, a time period characterised by considerably warmer temperatures than those experienced during the terminal Pleistocene. Despite an overall increase in temperature, climatic conditions still varied between regions. Evidence from Boomplaas indicates that rainfall in the southern region may have become increasingly seasonal at this time. With rainfall now largely limited to the summer months, the region became markedly drier, even experiencing periodic droughts during the rainy season (H. J. Deacon *et al.* 1984; Scholtz 1986). In the western region, faunal evidence at Elands Bay Cave suggests that relatively wet conditions prevailed during the transitional period (Klein 1984, 1986, 1991). Coastal morphology changed markedly as an increase in global climate melted the polar icecaps, thus causing higher ocean levels. Changes in terrestrial ecosystems were even more dramatic. Warmer, wetter conditions encouraged a reduction in grasslands and an increase in shrub and heath vegetation in the Fynbos Biome (J. Deacon and Lancaster 1988). This may have been one of the reasons for the extinction of megagrazers such as the giant Cape horse, *Equus capensis*, and giant buffalo, *Pelorovis antiquus* (Klein 1980, 1984b). Other large game became regionally less common particularly along the coastal margins. On the other hand, small to small-medium sized browsers became more numerous in the Fynbos Biome (Klein and Cruz-Uribe 1987).

Terminal Pleistocene/early Holocene assemblages in the Cape coastal regions still contain a high percentage of large grazing species compared to assemblages from later periods. The sites of Nelson Bay Cave and Elands Bay Cave provide evidence for the most recent occurrences of extinct grassland forms such as the Cape Horse (*Equus*

capensis), giant buffalo (*Pelarovis antiquus*) and Bond's springbok (*Antidorcas bondi*), post-dating 12 000 BP when these species had already become extinct in the interior (Klein 1980). Compared to the pre-12 000 BP period, assemblages now contained a greater number of non-gregarious small and medium sized ungulates. At Elands Bay Cave the extinct large grazers persisted until *ca.* 9600, but alongside an increase in small browsers such as steenbok (*Raphicerus campestris*) and grysbok (*Raphicerus melanotis*) (Klein 1980; Mitchell 1988). At Boomplaas, there was a clear shift in dominance from large grazing faunas to browsers and mixed feeders at *ca.* 9000 BP. (Klein 1978; Mitchell 1988). A similar pattern is evident at Nelson Bay Cave (Klein 1972a, b; 1980). At Melkhoutboom the shift from large grazers to small browsers had occurred relatively late at *ca.* 7500 BP (H. J. Deacon 1976). At Byneskranskop browsers started replacing grazers at more or less the same time as at Melkhoutboom (Klein 1981). With a rise in ocean levels approaching contemporary levels, many sites that are now situated close to the coast show an increase in the exploitation of marine resources. Mussels and limpets are present at most. At Elands Bay Cave, rock lobsters were extensively exploited at this time (Parkington 1981). Plant food residues remain relatively rare in Oakhurst assemblages. Fruiting species appear to have been most commonly consumed, while geophytes, a staple during later periods, are rarer (Mitchell 2002).

With the onset of more favourable climatic conditions after *ca.* 12 000 BP, there was a significant increase in human population numbers as reflected in the increase in archaeological occurrences compared to Robberg times. In addition to the continued occupation of large coastal rock shelters such as Nelson Bay Cave and Elands Bay Cave,

people started occupying previously neglected smaller shelters such as Matjes River Rock Shelter (Louw 1960; Vogel 1970). There was also a significant reoccupation of the South African interior. Sampson (1985), who had been unable to identify Robberg occurrences in the Seacow Valley, discovered many archaeological occurrences after *ca.* 12 000 BP. Though most of the open Lockshoek sites in the South African interior are undated, the well-dated sequence at Florisbad in the Free State indicates that the interior version of the Oakhurst had appeared relatively early on, at *ca.* 11 600 BP (Kuman and R. J. Clarke 1986).

THE MID-HOLOCENE TO LATE HOLOCENE:

THE WILTON COMPLEX: THE CLASSIC WILTON AND PRE-CERAMIC POST-CLASSIC WILTON INDUSTRIES

By *ca.* 8000 BP, the various regional variants of the Oakhurst Complex were replaced by the Holocene microlithic Wilton Complex across much of South Africa. Based on shifts in scraper morphology, and the relative frequencies of various types of backed microliths, three successive phases within the Wilton tradition are recognised today: (1) an early phase, transitional between Oakhurst and Wilton traditions (*ca.* 8000 – 7000 BP); (2) Classic Wilton assemblages that are characterised by high numbers of segments (*ca.* 7000 – 4000 BP); (3) and post-Classic Wilton assemblages (*ca.* 4000 – colonial period) that are characterised by an increase in the use of backed bladelets and points, the proliferation of adzes in certain regions, and the introduction of ceramics at *ca.* 2000 BP (J. Deacon 1972; Sampson 1974). This section will focus on the Classic Wilton and pre-ceramic Post-

classic Wilton. The ceramic containing post-Classic Wilton of the last 2000 years will be covered in the next section.

The advent of the Wilton varies considerably between regions. In the first analysis of the patterning of South African LSA radiocarbon dates, J. Deacon (1974) highlighted the abundance of mid-Holocene Wilton assemblages in the southern and eastern regions, and their virtual absence in the interior. At the time, she hypothesised that the rarity of mid-Holocene assemblages in the interior may reflect lower population densities, a result of the onset of arid climatic conditions (J. Deacon 1974). Until the 1980's, the only known interior sites with mid-Holocene Wilton assemblages were in the Drakensberg region in South Africa's eastern interior (Cable *et al.* 1980), and the Kuruman-Vryburg region in the Northern Cape (Humphreys and Thackeray 1983). Two of the earliest known Northern Cape sites with mid-Holocene Wilton assemblages are Wonderwerk Cave and Little Witkrans (Humphreys and Thackeray 1983). The mid-Holocene occupation hiatus in the South African interior initially appeared to have been longest in the north-eastern part of the country. However, during the 1980's, a number of new mid-Holocene Wilton assemblages were discovered in Gauteng Province and the Northern Province (Wadley 1986, 1987, 1989; Wadley and G. Turner 1987; Mason 1988). The site of Kruger Cave in the Northern Province was one of the first sites to provide evidence of mid-Holocene occupation of the north-eastern part of South Africa, with a date of *ca.* 7570 ± 100 BP (A. J. V. Brown and Verhagen 1985). In the Magaliesberg, a slightly later date of *ca.* 6490 BP was obtained for Jubilee Shelter (Wadley 1986). The nearby site of Cave James also produced a similar date to that of Jubilee Shelter (Wadley 1988). In the Thukela Basin in

KwaZulu-Natal a mid-Holocene occupation dating to *ca.* 7000 BP was identified by Mazel (1989, 1996). Other interior sites with mid-Holocene Wilton assemblages are the sites of Rose Cottage Cave (Wadley 2000 b) and Sehonghong (Mitchell 1996), both of which contain long LSA sequences. However, compared with the coast, mid-Holocene Wilton assemblages remain uncommon in the South African interior.

The vast majority of mid-Holocene Wilton assemblages occur in the southern and eastern regions. In these two regions, the Wilton appears at roughly the same time. At the sites of Nelson Bay Cave, Boomplaas and Kangara, J. Deacon (1984a) reports that Wilton tools were manufactured from *ca.* 7500 BP., however the incidence of formal tools only start to increase markedly between *ca.* 6000 and 6500 BP. At Matjes River Rock Shelter (Louw 1960; Vogel 1970; Döckel 1998) and Melkhoutboom (H. J. Deacon 1976), the start of the Wilton is also dated to *ca.* 7500 BP. As one moves towards the south-western and western regions, the distribution of mid-Holocene Wilton occurrences become patchy and rare. At Byneskranskop, segments were adopted relatively late at *ca.* 6500 BP (Schweitzer and Wilson 1982). At the site of Elands Bay Cave, there was a hiatus in occupation between *ca.* 7900 BP and 4300 BP, consequently, no mid-Holocene Wilton deposits are present (Parkington *et al.* 1987). There is also a hiatus at the nearby Tortoise Cave at approximately the same time (Robey 1987; Jerardino 1995). D. E. Miller *et al.* (1993) have suggested that people may have avoided this area due to possible negative effects that the mid-Holocene marine transgression may have had on coastal/estuarine productivity. That the hiatus was only a local phenomenon is suggested by the presence of a mid-Holocene occupation (*ca.* 6100 BP) at Steenbokfontein, a site further north of Elands Bay Cave (Jerardino and Yates 1996). A date of 5130 ± 50 BP had also been

obtained at Doorspring midden, close to Steenbokfontein (Kaplan 1994). Besides these two dates, there are no other reliably dated mid-Holocene occupations in the western region, suggesting sparse occupation.

Late Holocene post-Classic Wilton assemblages are far more common than mid-Holocene Classic Wilton assemblages. Along with intensified settlement of the southern and eastern regions, there was a marked increase in the occupation of the South African interior after *ca.* 4000 BP. In Namaqualand in the Northern Cape, there is no sign of LSA occupation during the mid-Holocene. At sites such as Spoegrivier (Vogel *et al.* 1997; Webley 2001) and Die Toon (Webley *et al.* 1993) human occupation starts at around *ca.* 3800 BP. In addition to the mid-Holocene Wilton occurrences at the Northern Cape interior sites of Wonderwerk Cave and Little Witkrans, additional late Holocene Wilton assemblages occur at Powerhouse Cave, Dikbosch 1 and 2 and Limerock 1 and 2 (Humphreys and Thackeray 1983). At Rose Cottage Cave in the Eastern Free State, there is a long break after the end of the Classic Wilton phase. A Post-Classic Wilton phase is present at this site at *ca.* 2200 BP (Wadley 1997). In the western and south-western regions where mid-Holocene occupation had been patchy, there is a proliferation of Wilton occurrences in rock shelters and open air sites. At *ca.* 4300 BP Elands Bay Cave was resettled (Parkington *et al.* 1987). The nearby Tortoise Cave was also resettled at around this time (Robey 1987; Jerardino 1995). At the site of Faraoskop, where there had been an even longer hiatus than at Elands Bay Cave, reoccupation commenced at *ca.* 4400 BP (Manhire 1993). Settlement in the Elands Bay area was mostly concentrated in caves and rock shelters between *ca.* 4300 BP and 2900 BP. At *ca.* 3000 BP, a number of

open air sites were added to the inventory of places where people preferred to settle. Between *ca.* 2900 BP and *ca.* 2100 BP, caves and shelters were apparently largely ignored for habitation, while open air sites close to the sea were preferred (Jerardino and Yates 1996). These enormous open air shell middens have been dubbed "megamiddens" (Buchanan 1988; Parkington *et al.* 1987). The few rock shelters that show human occupation during the "megamidden" period include Pancho's Kitchen Midden (Jerardino 1998) and Steenbokfontein (Jerardino and Yates 1996).

The Wilton is characterised by the manufacture of more formal stone tools than at any other time during the LSA. Artefacts manufactured during the Wilton include scrapers, backed microliths (bladelets and points), borers, reamers, adzes and milled pebbles, microliths with serrated edges, tanged points, grooved stones, sinkers and bored stones (J. Deacon 1984a). With the shift back to a microlithic stone tool tradition, there was a concurrent shift back to fine-grained raw materials. At the sites of Nelson Bay Cave, Boomplaas and Kangara, for instance, people preferred nodules, particularly local quartz, for the manufacture of Wilton tools (J. Deacon 1984a). At Rose Cottage Cave, nearly all formal tools were made out of local opalines during the Wilton, as was the case during the terminal Pleistocene Robberg (Wadley 2000b). Local opalines are similarly abundant at Sehonghong (Mitchell 1996). The use of fine-grained raw material and the microlithic nature of the flakes and formal tools produced during the Wilton, reminds one of the terminal Pleistocene Robberg. However, unlike the Robberg, the emphasis during the Wilton was not on the systematic production of bladelets. Instead, flakes were used to manufacture the backed microliths that characterise many Wilton assemblages.

Goodwin and Van Riet Lowe (1929) considered the presence of backed tools, particularly segments, as essential to the identification of Wilton assemblages. Segments, however, are more common in Classic Wilton assemblages than post-Classic Wilton assemblages. In addition, segments in Wilton assemblages display great interregional and intraregional variation. Backed tools, including segments, are very common at Wilton Large Rock Shelter, the Wilton type site (J. Deacon 1972). At sites such as Rose Cottage Cave (Wadley 2000b) and Sehonghong (Mitchell 1996), segments make up a smaller percentage within the formal tool class. Other mid-Holocene sites with significant numbers of segments include Jubilee Shelter (Wadley 1986), Uniondale (Leslie 1989), Oakhurst (Schrire 1962), Wonderwerk and Little Witkrans (Humphreys and Thackeray 1983). Interestingly, backed tools as a class are rare, or even absent at cave and rock shelter sites in the mid-to-late-Holocene of the western and south-western regions. These sites include Steenbokfontein (Jerardino and Yates 1996), Elands Bay Cave (Sievers 1977), Faraoskop (Manhire 1993) Pancho's Kitchen Midden (Jerardino 1998) and De Hangen (Parkington and Poggenpoel 1971). Segments and other backed tools only become common in some western and south-western region assemblages during the last 2000 years, as is attested to at Dune Field Midden (Parkington *et al.* 1992) and Vensterklipkop (Parkington 1977). In the southern and eastern regions, there is a reduction in the frequency of backed pieces in post-Classic Wilton assemblages and an increase in scrapers. This is evident at large sites such as Boomplaas (H. J. Deacon 1998) and Nelson Bay Cave (Inskeep 1987) and smaller sites such as Fairview (Robertshaw 1984; Hall 1985a), Strathalan Cave A (Opperman 1996), Ravenscraig (Opperman 1987) and Edgehill (Hall 1985b) to name a few.

Along with increased typological variability, there is evidence for greater regionalisation or localisation of stylistic trends during the late Holocene post-Classic Wilton (Hall 1990; Wadley 2000b). In the eastern region, hypothesised woodworking tools known as Kasouga flakes, are unique to the Uniondale area (Leslie 1989). Inland of the Tsitsikamma coast, microlithic (Wilton) assemblages occur along with distinctive macrolithic (Kabeljous) assemblages after *ca.* 4700 BP (Binneman 1996). Unlike the Classic Wilton, the macrolithic Kabeljous industry is relatively informal and is characterised by grooved stone sinkers, bored stones, grindstones, and most significantly, large quartzite segments. Binneman (1996) and Henderson and Binneman (1997) argue that the makers of the large quartzite segments of the Kabeljous industry, which is also present at Klasies River and along the Great Fish River, were groups permanently settled along the coast. On the other hand, the makers of the microlithic Wilton assemblages were people based in the Cape Fold Belt, who made seasonal visits to the coast (Binneman 1996). Binneman's (1996) argument is reminiscent of a model introduced by Inskeep (1987) in which he had suggested that seasonal visitors from the Cape Fold Belt and beyond were responsible for the manufacture of the microlithic Wilton at Nelson Bay Cave. Other signs of increased regionalisation include bifacially retouched points at Nelson Bay Cave (Inskeep 1987), bifacially retouched, pressure flaked bladelets in parts of Lesotho and the eastern Free State (Mitchell *et al.* 1994; Klatzow 1994, 1996; Mitchell 1999) and tanged points and arrow heads in the interior (D. Morris 1990; Humphreys 1991). In addition to tool styles, changes in raw material have also been suggested as evidence of regional stylistic markers. Hall (1990) notes that in the eastern extension of the Cape Fold Belt, the shift away from local hornfels to exotic silcretes after 5000 BP,

represents raw material taking on a role as a socio-spatial stylistic marker. By using a specific type of raw material, people would distinguish themselves from neighbouring groups. Raw materials have also been used as evidence for lower group mobility. At Blydefontein in the South African interior, Bousman (1991) demonstrated a gradual decrease in range size after *ca.* 4500 BP, based on the declining use of opalines from the Gariep River gravels.

With the onset of the Wilton, the variety of bone, ostrich eggshell and marine shell artefacts increased dramatically from pre-Wilton times. Preservation of organic material is less of a problem in these more recent sites, so wood artefacts, leather, and string manufactured from grass are more common. Some of the best preserved examples of preserved leather, string and digging sticks in the LSA come from the western region site of Faraoskop (Manhire 1993). Bone artefacts include fish hooks, arrow points, foreshafts, spatulas, spoons, beads, pendants and eyed needles. The presence of bone fish hooks, particularly at inland sites such as Rose Cottage Cave (Wadley 2000b) and various sites in Lesotho (Carter and Vogel 1974; Mitchell and Charles 1998), attest to the importance of aquatic resources in the diets of coastal people. There was also a proliferation of marine shell pendants, bone pendants, ostrich eggshell beads, bone beads and stone beads at this time. Hall and Binneman (1987) and Hall (2000) note that these are often included in great quantities as burial goods in the southern and eastern regions. In addition to pendants, marine shell tools have also been found at many sites mainly at the coast (Goodwin 1938; H. J. Deacon 1976; Schweitzer 1979; Manhire 1993; Jerardino 1998).

Ostrich eggshell water containers and tortoise shell food containers are also now common in assemblages.

There are no securely dated human burials in the Upper Pleniglacial. A human burial from Peer's Cave, that of the famous Fish Hoek Man, (Keith 1931) is estimated to have come from terminal Pleistocene context (J. Deacon and Wilson 1992). However, as mentioned, a radiocarbon date is yet to be published for this specimen. The earliest securely dated burials were discovered in early Holocene context at Matjes River Rock Shelter (Meiring 1937; Louw 1960; Protsch and Oberholzer 1975) and Elands Bay Cave (Parkington 1981). However, it is only from the mid-Holocene that there is a gradual increase in the number of burials. In the Fynbos Biome, the vast majority of early to mid-Holocene burials have been recovered from caves. Many of these, particularly in the eastern and southern regions, display extensive ritual elaboration with the inclusion of ochre and a myriad of grave goods (Inskeep 1986; Hall and Binneman 1987; Hall 1990, 2000). Ritual elaboration of graves reached its peak during the mid-Holocene. Hall (1990) notes that although burials from the Albany levels at Matjes River Rock Shelter contain burial goods such as bone and shell ornaments, and some also display ochre staining, these early burials are less elaborate than those from the mid-Holocene Wilton levels at the same site. At the site of Oakhurst, marine shell ornaments are relatively common inclusions in mid-Holocene graves (Goodwin 1938; Patrick 1989). Mid-Holocene burials at Klasies River and The Havens Cave contain strings of ochre stained ostrich eggshell beads, marine shell ornaments, and polished bone (Singer and Wymer 1982; Hall and Binneman 1987). Painted burial slabs also appear in some Wilton burials in the southern

and eastern regions (Dreyer 1933; Rudner 1971; H. J. Deacon *et al.* 1976; Binneman and Hall 1993; Binneman 1999). That burial slabs do not appear outside of these two regions suggest that they may have been another form of regional marker. In the western and south-western regions, cave burials are also relatively common. However, burials contain fewer grave goods than those in the southern and eastern regions (Hall and Binneman 1987). After *ca.* 3000 BP, many burials along South Africa's western, south-western and southern coasts were open dune cordon burials. In contrast to the coast, burials in the interior were rare during the Classic Wilton and post-Classic Wilton periods (A. G. Morris 1992a). Humphreys (1970, 1974) reports an isolated burial dated to 3360 ± 60 BP at Weltevreden in the Northern Cape Province that was buried with five ostrich eggshell beads and ochre. The sample of mid-Holocene burials from the interior is however too small to make concrete statements about the degree of elaboration. However, it is interesting to note that interior burials from the late Holocene are in many cases single occurrences in the open and generally lack the elaboration seen in mid-Holocene coastal burials (Inskeep 1986; A. G. Morris 1992a; Wadley 1996b). Then again, this is also true of late Holocene coastal burials along the west coast.

Hall (1990, 2000) has argued that cave burials in the southern and eastern regions were strategies used by groups to link themselves to a specific place, and in this way to distinguish themselves from other groups in an increasingly crowded landscape. After *ca.* 4000 BP continued economic and settlement intensification was facilitated by a conceptual change in the power of burials in the eastern region. Whereas during the early part of the mid-Holocene some sites were exclusively being used as cemeteries, after *ca.*

4000 BP these sites were being used as living areas as well as cemeteries. Hall (2000) argues that this was an even stronger affirmation of the link between a group and their territory.

Burials may also have reflected the increased stress that communities were feeling at the time. Many of the richly adorned graves from the southern and eastern regions were those of children (Hall and Binneman 1987). Hall and Binneman (1987) have hypothesised that this may reflect an early form of the Ju/'hoansi practice of grandparents passing *hxaro* goods (Wiessner 1977, 1982) to grandchildren not yet able to exchange them. Hall (1990) has argued that groups used gift exchange at this time as a means to build exchange ties between groups in an increasingly stressful environment. The importance that strong ties between groups may have had on group survival at this time cannot be overstated. In the western and south-western regions, skeletal evidence of increased interpersonal violence during the third millennium may represent the consequences of a breakdown of group ties at a time of increased competition for scarce resources (A. G. Morris and Parkington 1982; A. G. Morris *et al.* 1987; Pfeiffer *et al.* 1999; Pfeiffer and van der Merwe 2004).

Global temperatures increased dramatically and on a consistent basis between *ca.* 8000 B. P. and 6000 B. P., with all evidence pointing towards this period being the warmest since the Last Interglacial ended approximately 125 000 years ago (Shackleton and Opdyke 1976; Partridge *et al.* 1999). Accompanying this general increase in temperature were sea level increases which reached a maximum of about 2-3m above present levels (Reddering 1988; D. E. Miller *et al.* 1993; Compton 2001). The Karoo appears to have been

particularly arid at this time (H. J. Deacon 1972, 1976; Partridge *et al.* 1999). In the southern region, micromammal (Thackeray 1987) and charcoal analysis (Scholtz 1986) at Boomplaas show that the period *ca.* 6400 was the hottest of the entire sequence. Despite this, the Fold Belt mountains and coastal plains were still better-watered than the interior and consequently were continuously occupied during the last 10 000 years (J. Deacon 1974). The coastal and coastal forelands in the eastern region, which were also less arid at this time than the interior, also display a more or less continuous archaeological record throughout the Holocene (Hall 2000). The western and south-western regions on the other hand, experienced marked aridity. Micromammal species at Byneskranskop indicates the presence of dry conditions during the mid-Holocene (D. M. Avery 1982). At Elands Bay Cave and the nearby Tortoise Cave, there was a hiatus in occupation between *ca.* 7700 BP and 4400 BP (Parkington 1981; Robey 1987). As mentioned earlier, this probably has more to do with the negative effects that the mid-Holocene marine transgression had on coastal and estuarine productivity in the area than with arid climatic conditions (D. E. Miller *et al.* 1993). After *ca.* 4000 BP, cooler temperatures prevailed in the interior and along the coast (J. Deacon and Lancaster 1988). In the Fynbos Biome, micromammal species at Byneskranskop and Elands Bay Cave indicate the presence of moist conditions for the western and south-western regions respectively, while at Die Kelders in the southern region, conditions were cooler (D. M. Avery 1982, 1983).

As the mid-Holocene progressed, people placed an increasing emphasis on a broader spectrum of food resources. These include non-gregarious small and medium sized ungulates, ground game (molerats and hyraxes), tortoises, marine and riverine resources

and plant foods. At the same time, there was a de-emphasis of large game species. Changes in subsistence patterns did not occur all at once across all sites, but varied between sites, probably due to a combination of environmental and social factors. For instance, the shift from large grazers to small, closed-country browsing game occurred during the early Holocene at Boomplaas Cave (H. J. Deacon 1976), probably precipitated by an early reduction in grasslands and a concurrent expansion of closed bush. A similarly early change occurred at Nelson Bay Cave at *ca.* 9000 BP (Klein 1980). At Melkhoutboom and Byneskranskop, the change occurred later, at *ca.* 7500 BP, at the start of the Wilton (H. J. Deacon 1976; Klein 1981). The increased prevalence of small, closed country species, and absence of large, open grassland species, necessitated a change in hunting strategy. Consequently hunters made greater use of snares and other forms of traps (H. J. Deacon 1976). The absence of large grazers, particularly along the coast, led to increased dependence on ground game and tortoises in the mid-to-late Holocene diet. The numbers of rock hyrax and tortoise bones at De Hangen in the western region suggest heavy exploitation of these two species (Parkington and Poggenpoel 1971). At Elands Bay Cave and Tortoise Cave, tortoise and molerat remains are extremely common in assemblages prior to and after the mid-Holocene hiatuses in occupation (Klein and Cruz-Uribe 1987). Interestingly, tortoises are significantly smaller after *ca.* 4000 BP at these two sites, a phenomenon that Klein and Cruz-Uribe (1987) have attributed to increased exploitation due to an increase in human population numbers. This phenomenon is also evident at the southern region sites of Byneskranskop and Die Kelders Cave (Klein and Cruz-Uribe 1983). At interior sites the situation was slightly different than at the coast because of the persistence of grasslands and large grazers

throughout the Holocene. However, even here smaller animals were being taken in greater numbers during the Holocene, leading to more mixed faunal lists than the large grazer dominated faunal lists of the terminal Pleistocene. This pattern is evident at Rose Cottage Cave (Wadley 2000b) and Tloutle in Lesotho (Plug 1993), although at Sehonghong eland remained the most commonly hunted animal (Carter 1978).

At coastal sites the exploitation of marine resources such as shellfish, seals and marine birds multiplied exponentially during the mid-to-late Holocene. Huge shell middens accumulated in caves and rock shelters such as Elands Bay Cave (Parkington 1977; Parkington 1981), Nelson Bay Cave (Inskeep 1987), Matjes River Rock Shelter (Louw 1960; Döckel 1998), Steenbokfontein (Jerardino and Yates 1996) and Tortoise Cave (Jerardino 1995, 1996), as well as in the open. The increased emphasis on marine resources is typified by the appearance of large "megamiddens" along the coast at *ca.* 3000 BP (Binneman 1985; Parkington *et al.* 1987; Jerardino and Yates 1997; Jerardino 1998). Along with the remains of shellfish, "megamiddens" also contain the bones of small antelope, ground game and tortoises, as well as stone artefacts and other cultural objects (Jerardino 1998). Tortoise remains are especially numerous in "megamiddens", suggesting that these animals provided the bulk of the terrestrial meat at this time (Jerardino 1996; Jerardino and Yates 1996).

Evidence for plant food gathering is relatively scarce in South Africa's LSA archaeological record prior to the late Holocene. This may, in large part, be due to bad preservation in earlier archaeological occurrences. However, it may also point to an

increased emphasis on plant foods during later times. At Melkhoutboom, two species of geophytes, namely *Watsonia* and *Hypoxis*, became more conspicuous in mid-Holocene levels (H. J. Deacon 1976, 1993). This site provides some of the earliest evidence for plant food gathering by LSA people. Plant foods became progressively more common and eventually dominated food debris in later assemblages, particularly in those post-dating 2000 BP, as demonstrated at Scott's Cave in the Gamtoos Valley (H. J. Deacon and J. Deacon 1963; H. J. Deacon 1993) and at De Hangen in the western region (Parkington and Poggenpoel 1971). This could be viewed as evidence in support of fire-stick farming of geophytes, one of the food procurement activities that appeared to have increased as local hunting and gathering shifted in the direction of delayed returns. In an attempt to prolong access to plant resources, people made use of storage pits as is demonstrated at Melkhoutboom (H. J. Deacon 1976).

Based on research in the western and south-western regions, Parkington (1972, 1977, 1984a) suggested a model of seasonal mobility between coastal and inland resources for this region between *ca.* 4000 and 2000 BP. Using seasonal indicators such as the ages of seals and rock hyraxes, Parkington's model suggests that the coast was visited during the winter months, while people moved inland during the summer. However, later data on site occupations have indicated that settlement patterns were strongly coastally orientated during this time, as is suggested by the presence of "megamiddens". Stable carbon isotope analyses of coastal and inland human skeletons from this region also do not suggest movement between the coast and inland regions. On the contrary, coastal

skeletons display strongly marine orientated diets, while inland skeletons display strongly terrestrial diets (Sealy and van der Merwe 1986, 1988; Sealy *et al.* 1992, 2000).

In contrast to the patchy occupation of the South African interior and south-western and western regions, the Cape Fold Mountain Belt, southern and eastern regions remained relatively densely inhabited during the mid-Holocene. With a return to temperate climatic conditions after 4000 BP, humans started to resettle the inland regions of southern Africa. Increased ranging space however did not appear to relieve the increasing pressures being placed on coastal populations by population growth. Not only would high population density have placed strain on scarce food resources, but it would also have impinged on the mobility of groups. From the archaeological evidence described above, it is clear that dramatic changes were occurring in diet, social organisation and settlement pattern particularly after *ca.* 4000 BP (J. Deacon 1984b; Hall 1990; Binneman 1996). In the eastern region, a decrease in group mobility was accompanied by an increase in group interaction (Hall 1990; Binneman 1996). In the southern region, increased sedentism is suggested at the site of Nelson Bay Cave where increased exploitation of local raw material for tool production ensued at *ca.* 3300 BP (Inskeep 1987). In the western and south-western regions, there was the move towards large open air "megamidden" sites where huge quantities of marine shellfish were processed at *ca.* 3500 – 3000 BP (Parkington *et al.* 1987; Jerardino 1996, 1998; Jerardino and Yates 1997). Across the study region, people started exploiting a broader spectrum of food, possibly because of reduced home ranges and pressure being placed on food sources due to increasing population numbers. As mentioned above, the exploitation of small "packages" of protein

and plant foods increased dramatically after *ca.* 4000 BP. These dramatic changes are all expressions of a general trend towards resource intensification which began to characterise the lifestyles of populations during the latter half of the Holocene (Mazel 1989; Hall 1990; Binneman 1996).

POST-CLASSIC WILTON WITH POTTERY

By about 2000 BP, domestic sheep bones and ceramics make their appearance in the South African archaeological record (Robertshaw 1978; Barnard 1992). The wild progenitors of domestic sheep are not indigenous to Africa, but rather the Near East. Some of the earliest evidence of the presence of domestic sheep in Africa dates to *ca.* 7700 BP in the Sahara (Wendorf and Schild 1994). From here, sheep and other domesticates filtered down to southern Africa, probably through east Africa, where evidence of non-Bantu herding is well-documented by 4500-4000 BP (Ambrose 1982, 1984).

There are currently two theories about the manner in which herding reached South Africa. The older theory proposes that the historically recorded South African Khoekhoe pastoralists were the descendents of Hamitic pastoralists who moved southwards with their herds from their east African homelands. This theory has its roots in late 19th century ethnology which proposed that all human cultures had their origins in a single place. Since the ancestors of the Khoekhoe were hypothesised to have originated in the north-east of Africa, this theory became known as the "Hamitic" (after the name given to ancient East Africans) or "Erythriote" (after the name of the Red Sea) theory. Aspects of

material culture (Rudner 1968; A. B. Smith 1992), burial style (Dreyer and Meiring 1937) and language (Ehret 1973) hint at a possible connection between East and South Africa, but are not generally regarded as conclusive. For instance, Sadr (1998) has remarked that similarities in South and East African pottery are functional and not just stylistic. Burial styles are also known to display great variation even within the same biological population (Inskeep 1986; A. G. Morris 1992c). Putative linguistic links between Khoekhoe and East African populations are largely built on roots identified in hypothesised ancestral language forms and are thus not reliable (Borland 1986). Early physical anthropologists also identified physical similarities between the Khoekhoe and East Africans (Dreyer and Meiring 1937, 1952). The issue of a physical resemblance between East African pastoralist groups and South African Khoekhoe has been addressed in a more recent study, and found to be without basis (A. G. Morris 1984, 1992c). At a more general level, perhaps, genetic studies of recent populations continue to find links between some East Africans and South African Khoesan peoples (Cavalli-Sforza *et al.* 1994; Cruciani *et al.* 2002).

The second, more widely accepted model (amongst contemporary archaeologists) proposes that only the domestic stock and the knowledge associated with pastoralism diffused down into southern Africa from east Africa. Archaeological, linguistic and ethnographic evidence suggest that the immediate origins of historically recorded Khoekhoe pastoralists can probably be traced to a large area straddling southern Zimbabwe and northern Botswana where local hunter-gatherers first came in contact with stock owners from further north (N. J. Walker 1983). Linguistic similarities between

languages spoken by historic Cape Khoekhoe pastoralists and Tshu-Khwe speakers in northern Botswana (D. F. Bleek 1929; Westphal 1963; Elphick 1977), suggest that this region may have been central to the initial acculturation of southern African hunter-gatherers. It should be noted that this link is not incontrovertible since many Khoekhoe dialects disappeared before linguists had a chance to study them, thus preventing us from knowing the full linguistic range of Cape Khoekhoe languages (Inskeep 1978; J. Deacon 1984b).

From northern Botswana/southern Zimbabwe, two routes of dispersal into South Africa have been proposed. The first route, proposed by C. K. Cooke (1965), is broadly similar to that suggested earlier by Stow (1905). Based on environmental zones through which early stock could have moved most easily, and the distribution of rock paintings depicting sheep, Cooke's (1965) route proposes initial dispersal from Zimbabwe, across northern Botswana and northern Namibia, then south along the coast to the Cape of Good Hope and finally eastwards to the Eastern Cape Province. Cooke's route differs from that of Stow in that Stow suggested that the initial movement of herding into South Africa was initiated in East Africa and not from within southern Africa. A second route was proposed by Elphick (1977) using a combination of ethnographic observations and linguistic evidence from Westphal (1963). This route sees initial movement from central Botswana directly south to the Orange River. Here there is a divergence in the route, with an initial movement along the eastern margin of the Karoo to the Eastern Cape Province, from where the major movement was west along the coast towards the Cape of Good Hope. Movement along the east coast was restricted, possibly due to unfavourable

environmental conditions or the presence of competing Iron Age farming communities in this area. A subsequent movement is proposed which sees the spread of pastoralism along the Orange River in a westerly direction towards the Atlantic coast, and then north into Namibia and south towards the Cape of Good Hope.

It is currently not known how the introduction of herding may have affected the biology of local inhabitants - were two culturally and biologically distinct populations represented after 2000 BP (one herder and the other hunter-gatherer), or was there one homogenous population? Again, there are two schools of thought on this issue. One school proposes that hunter-gatherers and herders formed two mutually exclusive socio-economic groups after 2000 BP. This school is grounded in the view that genetically distinct pastoralists had migrated into South Africa at *ca.* 2000 BP (A. B. Smith 1983, 1986, 1990, 1992; A. B. Smith *et al.* 1991; Yates and A. B. Smith 1993). Cultural differences between hunter-gatherers and immigrant pastoralists are regarded as having been so great that it would have been difficult to have made the transition from one lifestyle to the other, especially in the direction of hunter-gatherer to pastoralist. This inability to alter lifestyles would largely have maintained any distinctions that may have existed between local hunter-gatherers and immigrant pastoralists, including biological distinctions after *ca.* 2000 BP. The other school questions this rigid view, since there are historic and recent examples of hunter-gatherers having become herders (Hitchcock and Ebert 1984; J. B. Wright 1971). Instead, this school proposes that after the introduction of herding at *ca.* 2000 BP, hunter-gatherers and herders were essentially segments of a culturally and biologically homogenous population. The only difference, compared with pre-2000 BP times, was

that people now moved back and forth between hunting-and-gathering and herding (Marks 1972; Schrire 1980, 1992; Elphick 1985; Schrire and J. Deacon 1989). Within this scheme, hunting-and-gathering is viewed as a "down" phase (Elphick 1985). According to the adherents of this school, herding could have entered the region either by the acculturation of indigenous hunter-gatherer communities (Kinahan 1991), or via migrant pastoralist groups who mixed genetically with local populations, resulting in a genetically and culturally homogenous population in a relatively short time after arrival (Elphick 1977, 1985). This school views historically recorded Cape pastoralism as largely an *in situ* South African development. Sadr (1998) and Sadr *et al.* (2003) have suggested that the ideological barrier associated with the shift to herding may not have been that great in South Africa, because many communities, particularly in the Fynbos Biome, may already have been predisposed to herding. With local coastal inhabitants already having shifted to more delayed return socio-economic systems, an artefact of the intensification process that began *ca.* 4000 BP, the incorporation of a herding component may have been a natural progression (Sadr 1998). Not all adherents to *in situ* development believe that the Khoesan were biologically homogenous throughout the last 2000 years though. Some have argued that differentiation had indeed occurred between hunter-gatherers and herders, but that it was due to increasing socio-cultural isolation of herders from hunter-gatherers over the last 2000 years (Rightmire 1970, 1976, 1978; Hausman 1980, 1982, 1984). The issue of one homogenous or two distinct populations in South Africa after 2000 BP is a central theme of archaeological research focussing on the late Holocene.

Historical evidence is inconclusive as to whether hunter-gatherer groups and pastoralist Khoekhoe communities were distinct from one another. The position of people without livestock is especially pertinent here. These people, referred to as "Soaqua" or "Sonqua", have either been described in historical documents as poorer segments of a single hierarchical community (Schrire 1980; Elphick 1985), or as hunter-gatherers separate from the pastoralist communities (Parkington 1984b). Parkington and Hall (1987) have argued that Soaqua hunter-gatherers were pushed to the edges of society after the introduction of herding at the Cape. The increase in herder numbers, as well as the increase in stock, are said to have forced wild game, as well as hunter-gatherers out of higher nutrient coastal forelands, towards the more marginal inland mountainous regions (Parkington and Hall 1987). The archaeological record is generally unclear on the existence of two distinct communities during prehistoric times though. It has proven exceedingly difficult to distinguish between sites occupied by herders and those occupied by hunter-gatherers (Sadr 1998). Traces of prehistoric herders are often quite ephemeral, and do not resemble the sophisticated cattle herding societies that European colonists described on their arrival at the Cape.

Sheep and ceramics were initially thought to have been introduced simultaneously at *ca.* 2000 BP as part of a cultural "package" (Klein 1986). Prior to the widespread availability of accelerator mass spectrometry (AMS) dates, indirect dates from sites such as Die Kelders (Schweitzer 1979), Byneskranskop (Schweitzer 1979), and Nelson Bay Cave (Inskeep 1987), supported such a pairing. Early dates were rarely "direct" dates on sheep bones because these are normally too small for conventional radiocarbon dating. Rather,

sheep and pottery were routinely indirectly dated by their association with dated stratigraphic units. This method produced dates for the earliest appearance of sheep of 1960 ± 85 BP at Die Kelders (Schweitzer 1974), 1880 ± 50 BP at Byneskranskop (Schweitzer and Wilson 1982) and 1930 ± 60 BP at Nelson Bay Cave (Inskeep 1987). Disparities between indirect and direct dates became apparent though, when direct dates on sheep bone started appearing in the literature. Direct dates routinely indicated that sheep arrived much later at most sites than had previously been thought. Because of their small size, sheep bones tend to migrate down into older levels, leading to erroneous associations, and hence misleading dates. For instance, a sheep bone recovered from a level dated to 1930 ± 60 BP at Nelson Bay Cave yielded a direct date on bone collagen of 1100 ± 80 BP (Gowlett *et al.* 1987; Inskeep 1987). Sheep bones from the south-western region site of Kasteelberg A that had previously been thought to date to *ca.* 2000 BP were directly dated to 1630 ± 60 BP (Sealy and Yates 1994, 1996). In fact, the Kasteelberg A date was the oldest reliable date for the first appearance of sheep in the Fynbos Biome until the later discovery of, and direct dating of sheep bones at Blombos Cave to 1960 ± 50 BP and 1880 ± 55 BP (Henshilwood 1996). In the Northern Cape, dates are generally earlier than those from the Fynbos Biome. The western Northern Cape Province sites of /Ai tomas, with a date of 1980 ± 120 BP (Webley 1992a), and Spoegrivier, with dates of 1920 ± 40 BP (Webley 1992a 1992b, 2001; Vogel *et al.* 1997) and 2105 ± 65 BP (Sealy and Yates 1994), provide some of the earliest reliable dates for the presence of sheep in South Africa. A less reliable date was achieved for four sheep bone fragments which were recovered from deposits dated to 2400 BP at Spoegrivier (Webley 2001). The *ca.* 2000 BP dates for sheep are not the norm in the South African archaeological record. On

the contrary, most dates are around 1600 BP or younger (Vogel and Visser 1981; Gowlett *et al.* 1987; Inskeep 1987; Sealy and Yates 1994, 1996).

Ceramics, which are often fragmentary when found, are just as likely as sheep bones to migrate down the stratigraphic sequence and settle in older levels. Unlike sheep bones though, ceramics are much harder to date directly. Most of the dates that are available for ceramics are by association with dated levels. Based on the earliest non-direct dates then, the earliest examples of ceramics in South Africa come from sites in the Fynbos Biome. At the sites of Die Kelders (Schweitzer 1979), Nelson Bay Cave (Inskeep 1987), Byneskranskop 1 (Schweitzer 1979) and Blombos Cave (Henshilwood 1996), the appearance of ceramics date to *ca.* 2000 BP. At Die Kelders, this early date is more reliable than at other sites, since the cave has yielded almost 1000 sherds from a level dated to 1960 ± 85 BP. It is inconceivable that this number of objects could have migrated down through the deposit, given the relatively clear separations between stratigraphic layers reported by the excavators. Sherds are much sparser at the other three sites, which may be problematic in terms of the reliability of dates. At other sites in the region such as Kasteelberg A/lower Kasteelberg B (Sadr and A. B. Smith 1991), ceramics only became common approximately 400 years later, at *ca.* 1600 BP. As indicated above, this is also when sheep become most abundant in the archaeological record. It is currently not possible to determine beyond doubt whether ceramics and sheep arrived as a package at *ca.* 2000 BP from elsewhere. Single occurrences of sheep and ceramics appear at a few sites at *ca.* 2000 BP. However, a few inconsistencies exist, particularly relating to the ceramic record. For instance, the *ca.* 2000 BP ceramics at Die Kelders differ significantly

from ceramics found after *ca.* 1600 BP. Unlike later ceramics which are usually well-fired and thin-walled, those found in the *ca.* 2000 BP levels at Die Kelders are often thick-walled and fired at low temperatures (Schweitzer 1979). This raises a question about the likelihood that pottery was independently developed in South Africa. Also, if pastoralists migrated to South Africa from a hypothesised northern Botswana/southern Zimbabwe homeland, and brought with them their distinctive culture, one would expect stylistic similarities between ceramics in South Africa and ceramics in their land of origin. As Sadr (1998) has illustrated, radical differences in vessel shape, rim profile and decoration suggests that no such link exists between these regions. To resolve the issue of a simultaneous introduction of sheep and ceramics by a migrant population, more sites need to be excavated. Also, more direct dating needs to be performed on sheep, and particularly on ceramics.

The introduction of domesticates and ceramics did not accompany a change in stone tool manufacturing tradition (J. Deacon 1984a). There were minor shifts at some sites involving the relative frequency of some formal tools and the size and shape of scrapers, however, the general impression is one of continuity with the pre-pottery Wilton. There was nonetheless greater variation between assemblages than was previously the case. At Boomplaas Cave, there was continuity in scraper lengths and backed microlith numbers between pre-2000 BP and post-2000 BP levels (H. J. Deacon *et al.* 1978). At Witklip (A. B. Smith *et al.* 1991) and other western and south-western region sites (Mazel and Parkington 1978), adze production increased. There is generally a reduction in the manufacture of backed microliths across South Africa at this time. This does not appear

to have been the case along the west coast though. As previously mentioned, backed tools including segments become more common in west coast sites after 2000 BP (Parkington 1980). At the site of Dune Field Midden, backed tools compose 73% of the retouched tools category (Parkington *et al.* 1992). In the informal tool category, many coastal sites also possess large unretouched flakes and flaked cobbles (Sampson 1974).

Besides the inclusion of domesticates, the range of foods in the diets of post-2000 BP people appears to have changed little from pre-ceramic Wilton times. Stable isotope analysis of human skeletons post-dating 2000 BP indicate that the proportions of foods consumed did change, with people taking in less sea food, and relying more on terrestrial foods such as small antelope, tortoises and ground game (Sealy and van der Merwe 1988; Sealy and Pfeiffer 2000). The reduction in importance of marine foods is reflected in the archaeological record by the complete abandonment of megamiddens in the western

Criterion	**Pastoral assemblages**	**Hunter-gatherer assemblages**
Formal stone tools	Rare	Relatively common
Utilisation of-fine grained rock	Rare	Common
Abundance of grindstones	Common	Rare
Abundance of ceramics	Common > 700/m³	Few ≤ 10/m³
Presence/absence of *Donex* shell scrapers	Absent	Present
Size of ostrich eggshell beads	Large > 4.5 mm	Small < 5 mm though becoming larger after 1400 BP
Abundance of wild ungulates	Rare	Common
Abundance of sheep	Common	Rare
Abundance of seals	Common	Rare

Table 5.2: Criteria used to distinguish pastoral and hunter-gatherer sites in the south-western Cape (A. B. Smith *et al.* 1991).

and south-western regions after 2000 BP (Jerardino and Yates 1997; Jerardino 1998, 2003). Plant food gathering appears to have taken on an even more important role after 2000 BP. Sites such as Scott's Cave (H. J. Deacon and J. Deacon 1963; H. J. Deacon 1993), Melkhoutboom Cave (H. J. Deacon 1976) and De Hangen (Parkington and Poggenpoel 1971) contain dense layers of geophyte remains.

As mentioned earlier, the archaeological record does not show evidence for the existence of pastoralist societies of the scale recorded during historical times. Some sites do record the presence of sheep and pottery, but even in these cases, it is hard to determine whether the sites had been inhabited by pastoralists, or whether they had been inhabited by hunter-gatherers that had obtained stock via theft or exchange. Excavations by Schrire at Oudepost, a Dutch East India Company outpost, appeared to prove as much (Schrire and J. Deacon 1989). Historical documentation recorded the interaction between Dutch soldiers and Khoekhoe pastoralists at Oudepost. An analysis of stone tools from this site by Schrire and J. Deacon (1989) indicated that the flaked stone artefacts were indistinguishable from Wilton assemblages that archaeologists normally associate with hunter-gatherers. As a counter to this, A. B. Smith *et al.* (1991) collected data on the contents of several sites post-dating 2000 BP. From this they developed criteria which, they argued, distinguish between pastoralist and hunter-gatherer sites (Table 5.2).

A. B. Smith *et al.* (1991) have since been criticised because few sites comply entirely with their criteria. Schrire (1992) notes that there is too much overlap in the data from their two kinds of sites to be able to confirm or deny the existence of two distinct

populations. She also questions why differences between sites should reflect cultural differences instead of behavioural differences (Schrire 1992). Wilson (1996) notes that in the post-2000 BP levels at Die Kelders, the low incidence of formal tools and the presence of sheep and potsherds is consistent with herder occupation. However, where the frequency of potsherds and the size of ostrich eggshell beads are concerned, Die Kelders resembles a hunter-gatherer site. Based on the criteria of A. B. Smith *et al.* (1991) therefore, Wilson (1996) concludes that these Die Kelders levels cannot be classified as either hunter-gatherer or herder. At Jakkalsberg in the Northern Cape, a similar situation exists with sheep and an informal stone tool assemblage being consistent with a herder site, and the small size of ostrich eggshell beads and low ceramic density, not (Webley 1997). The ambiguity of the archaeological record, and the fact that it does not reflect the presence of a complicated pastoralist society, caused some to question whether the presence of sheep and pottery in assemblages should be attributed to the historically recorded Khoekhoe pastoralist societies (Sadr 1998; Sadr *et al.* 2003). These authors argue that the small scale sheep herding, which appears from the sparse archaeological remains to have characterised early herding in the region, is better interpreted as indigenous hunter-gatherers adding a herding component to their foraging activities and not evidence of immigrants. In this scenario, the hierarchical Khoekhoe societies from the historical period would be a later development.

The archaeological record may not be ideal for finding evidence of migrations. J. Deacon (1984a) notes that it has proved difficult to identify the presence of a migrant population on archaeological evidence alone, even in circumstances where there is good historical

evidence for migrations having taken place. The reason for this is that there are no concrete criteria by which to recognise migrations archaeologically. Specific criteria such as burial style may vary according to time, place and environment. The task would be particularly difficult if the immigrant population happened to have subsistence patterns and technology similar to those of the existing populations. The only time that local coastal populations in the research region certainly came into contact with immigrants was when Negroid farmers settled on the south-east coast of South Africa after migrating down the African east coast. Gene flow between local hunter-gatherers and immigrant farmers in this region is attested to by historic accounts of mixed Khoekhoe/Xhosa peoples called the Gonaqua (Giliomee 1979; Peires 1981), and the presence of many Khoesan derived click sounds in Nguni languages from this region (Knight *et al.* 2003; Traunmüller 2003).

SUMMARY

The South African LSA was extremely dynamic in terms of changes in stone tool technology and subsistence strategies. Notwithstanding early studies which interpreted cultural change in terms of human migrations, current archaeological research suggests that cultural variability prior to *ca.* 2000 BP was more likely the result of *in situ* developments. It is currently still unclear whether the introduction of domesticates and ceramics at *ca.* 2000 BP was accomplished by diffusion, or the migration of biologically distinct pastoralists into South Africa.

The first concrete alternative to the migration hypothesis was the Deacon model of homeostatic plateaux where variation in the LSA was interpreted in terms of sequential change (H. J. Deacon 1976; J. Deacon 1984a). Based on changes in stone tool assemblages and subsistence, the LSA was divided into three stages: (1) the Robberg Industry (*ca.* 22 000 – *ca.*12 000 BP); (2) the Oakhurst Complex (*ca.* 12 000 – *ca.* 8000 BP); and (3) the Wilton Complex (*ca.* 8000 – colonial period) respectively (H. J. Deacon 1976). These three stages represent periods during which the adaptive responses of people to their environment were hypothesised to have been relatively stable, with shifts required at *ca.* 12 000 BP and *ca.* 8000 BP due to changes in environmental conditions. This model still forms the basis of the conventional subdivision of the South African LSA.

The Robberg, which is primarily a microlithic industry that is dominated by bladelets, represents the first widely occurring LSA technology in southern Africa. The scarcity of archaeological occupations on the southern African subcontinent dating to the early part of the Robberg (*ca.* 20 000 – *ca.* 15 000 BP), suggests that human population size and distribution experienced a major decline during, and immediately after the LGM. At this time, human populations were primarily concentrated in the southern and eastern regions and largely avoided the interior. Faunal lists reflect the dominance of large grazers on the terminal Pleistocene landscape, giving rise to early interpretations of Robberg people as mobile big game hunters. Recent research has tempered this view, painting a more complex picture of subsistence. After *ca.* 15 000 BP, there was an amelioration of

conditions and human population levels gradually recovered. Previously unoccupied areas, including the interior were reoccupied.

Climatically, the terminal Pleistocene/early Holocene transition was marked by the onset of the current interglacial, a time period characterized by considerably warmer temperatures than those experienced during the terminal Pleistocene. This precipitated the extinction of megagrazers and their replacement by non-gregarious small and medium sized ungulates. During this time, the Robberg Industry was replaced by the Oakhurst Complex, including its various regional variants, across large parts of the country. Unlike the Robberg, the Oakhurst is overwhelmingly non-microlithic. It is typically characterised by large scrapers, large adzes and very few backed tools. With the onset of more favourable climatic conditions, human population numbers increased significantly from previous levels. The first evidence for deliberate burials in the South African archaeological record also occurs during this period. Associated with the burials at the site of Matjes River Rock Shelter are ochre and grave goods which indicate that the inhabitants possessed complex religious beliefs.

Global temperatures increased significantly and on a consistent basis between *ca.* 8000 and *ca.* 6000 BP. During this period, the interior became increasingly arid and shows signs of reduced habitation. The Fynbos Biome, particularly the southern region, was comparatively better watered, leading to a concentration of human populations in these areas. At *ca.* 8000 BP the Oakhurst Complex was gradually replaced by the Wilton Complex. Like the Robberg, the Wilton is overwhelmingly a microlithic industry. It is

characterised by a greater number of formal tools, particularly backed pieces, than both the Robberg and the Oakhurst. It is also characterised by a proliferation of non-lithic artefacts, some of which were not present in the two previous industries. Cave burials not only become more common in the Fynbos Biome, but they also displayed increasing elaboration with the inclusion of jewellery and other grave goods in the southern and eastern regions.

By *ca.* 6000 BP, there was a return to temperate climatic conditions. Gradually, people started resettling the interior of the country. Increased ranging space however did not appear to relieve the increasing pressure being place on populations in the Fynbos Biome by population growth. Not only would high population density have put strain on scarce food resources, but it would also have impinged on the mobility of groups. Archaeological evidence suggests that in response, dramatic changes occurred in diet, social organisation and settlement patterns at or just prior to 4000 BP. Probably because of reduced home ranges and pressure being placed on scarce resources, people started exploiting a broader spectrum of food. The exploitation of small "packages" of food such as tortoises, crustaceans, fish and mussels increased dramatically. Activities such as firestick-farming of geophytes may have come to characterise food procurement strategies as local hunting and gathering shifted in the direction of delayed returns. Technologically, this period was characterised by post-Classic Wilton assemblages. At many sites, there was a decrease in the manufacture of backed pieces and a greater presence of adzes, possibly reflecting increased geophyte exploitation.

By approximately 2000 BP, domesticates such as sheep, as well as ceramics, enter the archaeological record. Archaeological, linguistic, and ethnographic evidence suggest that the origins of Cape Khoekhoe pastoralism can probably be traced to a large area straddling southern Zimbabwe and northern Botswana where local hunter-gatherers first came in contact with stock owners from further north. The method by which herding was introduced to South Africa is still unclear. One school proposes that the migration of distinct herding communities into South Africa at *ca.* 2000 BP provides the most probable explanation for the appearance of domesticates. The alternative school proposes that the development of pastoralism in South Africa was largely an *in situ* phenomenon. According to this school, herding may have entered the region either by the acculturation of indigenous hunter-gatherer communities, or via migrant pastoralist groups who mixed genetically with local populations, resulting in a genetically and culturally homogenous population in a relatively short time after arrival. The only difference from pre-2000 BP times was that people now moved back and forth between hunting-and-gathering and herding. Results from archaeological excavations have thus far been ambiguous on the method of introduction, as well as on whether distinct pastoralist and hunter-gatherer communities existed during prehistoric times. The only time that we can be confident that populations in the research region came into contact with immigrants was when Negroid farmers moved into the south-eastern coast and near coastal regions of South Africa.

In this chapter, I purposefully presented an in depth review of the southern African LSA, since it is important to view biological change in human populations in a wider context. The environments in which human populations live often have a profound influence on

their biology. Changes in demography, technology, subsistence strategies and environment, factors which are often recorded in the archaeological record, may reflect incidences of biological change in a population. Since changes in the archaeological record may be very subtle, it is considered necessary to review as much available data as possible so that informed hypotheses on biological evolution may be constructed. The next section presents the hypotheses to be tested in the latter part of this thesis. These are constructed on the basis of the cultural information reviewed in this chapter and fossil evidence reviewed in the previous chapter.

HYPOTHESES

THE ANTIQUITY OF KHOESAN CRANIOFACIAL MORPHOLOGY

The first hypothesis centres on the antiquity of Khoesan craniofacial morphology. The craniofacial morphology of these early South African human populations has previously been described as large and robust, but essentially Khoesan-like (de Villiers 1974; Braüer and Rösing 1989). Large size and robusticity are not traits normally associated with the craniofacial morphology of recent Khoesan populations though. The only previously known complete South African specimen from this early period, the terminal Late Pleistocene Fishhoek cranium (SAM-AP 4692), is said to combine a mosaic of "Khoisanoid" (mainly facial) and "non-Khoisanoid" features (mainly cranial vault and overall robusticity) (Howells 1969; Rightmire 1974). The Albany man cranium (UCT 378) is also said to combine "Khoisanoid" features in the face with high levels of overall cranial robusticity (Braüer and Rösing 1989). Similar levels of robusticity are present in several calottes from Matjes River Level D (*ca.* terminal Late Pleistocene/very early

Holocene). Although these early crania are said to resemble recent Khoesan populations in certain aspects of craniofacial morphology, their apparent large size and robust features are thought to distinguish them from the crania of more recent populations (Braüer and Rösing 1989). The morphological affinities of these early specimens have however never been tested using a large sample of fully dated, complete crania.

Hypothesis 1: Antiquity of Khoesan craniofacial morphology. **Terminal Pleistocene/early Holocene populations possessed typical Khoesan craniofacial morphology.**

Sub-hypothesis 1a: Morphological homogeneity in the pre-5000 BP period. **There are no statistically significant morphological differences between crania in the pre-5000 BP sample.**

Sub-hypothesis 1b: Morphological continuity between pre-5000 BP and 5000 – 2000 BP populations. **Pre-5000 BP crania fall within the range of morphological variation of crania in the 5000 – 2000 BP cranial sample.**

FLUCTUATIONS IN BODY SIZE

Pfeiffer and Sealy's (2006) study of Holocene post-cranial remains from the Fynbos Biome highlighted stature fluctuations in foragers from this region over the last 10 000 years. This study demonstrated: (1) heightened stature levels prior to 4000 BP; (2) a dramatic decrease in stature between 4000 and 3000 BP; and (3) a recovery in stature levels after 3000 BP (Pfeiffer and Sealy 2006). In turn, previous studies on Pleistocene/early Holocene cranial remains have identified relatively large cranial size

and robust craniofacial morphology in early Holocene Khoesan populations, and small, more gracile cranial morphology in later Holocene populations (Bräuer and Rösing 1989). Unlike Pfeiffer and Sealy's (2006) study on the post-cranial remains though, there has never been a temporal assessment of Khoesan cranial size change during the Holocene. There is thus no way of knowing whether an apparent reduction in cranial size and robusticity levels displayed by Khoesan populations during the latter half of the Holocene (Braüer and Rösing 1989) was linked to a general reduction in body size between 4000 and 3000 BP, as suggested by the post-cranial skeleton (Pfeiffer and Sealy 2006). Hypothesis 2 investigates fluctuations in cranial size during the Holocene.

Hypothesis 2: Fluctuations in cranial size during the Holocene. **Cranial size is smallest between 4000 and 3000 BP.**

Sub-hypothesis 2a: Reductions in male cranial size. **Male cranial size is smallest between 4000 and 3000 BP.**

Sub-hypothesis 2b: Reductions in female cranial size. **Female cranial size is smallest between 4000 and 3000 BP.**

THE INTRODUCTION OF HERDING AND THE QUESTION OF BIOLOGICAL CONTINUITY IN LOCAL POPULATIONS

A major change in subsistence strategy occurred at approximately 2000 BP with the introduction of herding (Robertshaw 1978; Barnard 1992). Although some have claimed that herding was introduced to South Africa by culturally and biologically distinct immigrant herder populations at *ca.* 2000 BP (A. B. Smith *et al.* 1991; P. Smith *et al.*

1992), there is currently no unambiguous archaeological or physical anthropological evidence that such an immigration had ever occurred. Rather, the archaeological evidence is more conducive to a situation where herding diffused slowly into the region and was taken up by indigenous hunter-gatherers (Sadr 1998; Sadr *et al.* 2003). Indeed, hunting-and-gathering persisted alongside herding until colonial times. The long-term co-existence of these two subsistence strategies has led to further disagreement concerning the socio-economic and biological status of hunters and herders. One school of thought adheres to the view that hunters and herders formed two mutually exclusive socio-economic and biological groups (A. Smith 1983, 1986, 1990, 1992; A. Smith *et al.* 1991; Yates and A. Smith 1993, P. Smith *et al.* 1992). The other school of thought proposes that hunter-gatherers and pastoralists were segments of the same biological population moving back and forth between different economic strategies, rather than biologically or culturally distinct groups (Marks 1972; Schrire 1980, 1992; Elphick 1985; Schrire and J. Deacon 1989). This section investigates the related issues of biological continuity in local Khoesan populations at the onset of herding, and the biological homogeneity of post-2000 BP populations. Together these issues will inform on the question of whether Khoekhoe herders and San hunter-gatherers were biologically distinct populations or economic segments of the same biological population.

Hypothesis 3: Biological continuity at 2000 BP. **There is biological continuity between pre-2000 BP and post-2000 BP populations.**

Sub-hypothesis 3a: Inter-individual variation in males. **Inter-individual cranial variation did not increase in males at 2000 BP.**

Sub-hypothesis 3b: Inter-individual variation in females. **Inter-individual cranial variation did not increase in females at 2000 BP.**

Sub-hypothesis 3c: Form changes in males. **There are no significant changes in male craniofacial form at 2000 BP.**

Sub-hypothesis 3d: Form changes in females. **There are no significant changes in female craniofacial form at 2000 BP.**

Sub-hypothesis 3e: Allometric shape changes in male crania during the Holocene. **The major variation in male craniofacial shape during the Holocene is due to allometric scaling.**

Sub-hypothesis 3f: Allometric shape changes in female crania during the Holocene. **The major variation in female craniofacial shape during the Holocene is due to allometric scaling.**

CHAPTER SIX
MATERIALS AND METHODS

CRANIAL SAMPLE

The study sample consists of 153 crania (Table 6.1). Five criteria were used in the selection of this sample. First, to avoid juvenile cranial features influencing results, only crania from adult individuals were included i.e. the third molar had to be fully erupted and the basicranial suture fully fused; second, to avoid the negative effects that missing data might have on the significance of statistical analyses, each cranium had to possess all measurement landmarks; third, to avoid analysis of genetically mixed colonial samples, only crania older than 500 BP where included; fourth, cairn burials from the eastern region were not included since these probably represent the burials of Gonaqua (genetically mixed Negroid/Khoekhoe) individuals (Sealy and Pfeiffer pers. comm.); and fifth, to be able to position each specimen in geographic space, its place of origin had to be known.

The cranial sample originates from that section of the South African coastline south of 28°S and west of 30°E (Figure 6.1). The majority of the sample originally derived from the coasts and coastal forelands of the south-western and southern regions. Fewer crania were derived from the Cape Fold Mountain belt and the western and eastern regions. In the extreme northern part of the western region where the Cape Fold Mountain belt is not present, most crania were derived from burials within 1km of the ocean. In the eastern

Region	Accession no.	Sex	Locality	Date (BP)	Laboratory no.	Reference
Western Region	**SAM -AP 1446**	M	Port Nolloth	740 ± 30	Pta-9085	This study
	UCT 227	M	Watterbakke, near Lutzville	1000 ± 50	Pta-4405	[8]
	UCT 429	M	Elandsbaai	1870 ± 35	Pta-8814	This study
	UCT 387	M	Faraoskop	2055 ± 40	GrA-23218	This study
	UCT 164	F	Kleinzee, north of Buffel's River Mouth	2360 ± 30	Pta-8750	This study
	SAM -AP 5069	F	Doringbaai	2634 ± 28	OxA-V-2066-34	This study
	UCT 445	M	Groenrivier	2720 ± 60	Pta-5617	[1]
	SAM-AP 4931	M	Kleinsee	3750 ± 60	Pta-4827	[1]
South-Western	**SAM -AP 4867**	M	Vredenberg	590 ± 45	Pta-4407	[1]
Region	**SAM -AP 6020**	M	Tikosklip, Sadanha	620 ± 30	Pta-4189	[4, 5]
	SAM -AP 5035a	M	Melkbosstrand	620 ± 35	Pta-4401	[4, 5]
	SAM -AP 5032	M	Milnerton Beach	765 ± 25	OxA-V-2056-35	This study
	SAM -AP 5012	F	Langebaan	812 ± 26	OxA-V-2065-36	This study
	UCT 60	M	Saldanha	950 ± 50	Pta-2005	[1, 5]
	SAM -AP 6332	M	Melkbosstrand	980 ± 50	Pta-8767	This study
	SAM -AP 1247a	F	Blaawberg	1180 ± 50	Pta-4281	[4, 5]
	SAM -AP 4905	M	Blouberg Strand	1210 ± 50	Pta-4349	[4, 5]
	UCT 94	F	Klein Melkbos	1270 ± 40	GrA-23216	This study
	SAM -AP 4314	F	Noordhoek	1319 ± 25	OxA-V-2066-26	This study
	SAM -AP 6075	F	Saldanha	1330 ± 40	Pta-4186	[4, 5]
	SAM -AP 4669	F	Gordon's Bay	1333 ± 25	OxA-V-2056-28	This study
	SAM -AP 6074	M	Saldanha	1360 ± 40	Pta-4148	[4, 5]
	SAM -AP 4920a	F	Bloubergstrand, Melkbos Road	1364 ± 32	OxA-V-2059-17	This study
	SAM -AP 5034	F	Houtbay	1390 ± 40	Pta-4771	[4]
	SAM -AP 6334	M	Melkbosstrand	1400 ± 50	Pta-8790	This study
	SAM -AP 6149	M	Ouskip caravan park, Melkbos	1440 ± 70	Gx-13182	[4, 5]
	SAM -AP 5083	M	Ysterfontein, Darling	1490 ± 50	Pta-926	[4, 5]
	UCT 55	F	Blouberg Strand	1680 ± 40	GrA-23075	This study
	SAM -AP 4630	M	Sandy Bay	1775 ± 80	Gx-13178	[4, 5]
	SAM -AP 4659	F	Melkbos	1815 ± 29	OxA-V-2056-43	This study
	SAM -AP 6041a	M	Milnerton	1824 ± 27	OxA-V-2056-27	This study
	SAM -AP 4901	M	Pearly Beach	1892 ± 28	OxA-V-2065-40	This study
	SAM -AP 6264	M	Melkbosstrand	1950 ± 60	Pta-9073	This study
	UCT 120	F	Llundudno/Hout Bay	1960 ± 50	Pta-5677	[3]
	SAM -AP 3053	M	Strand, Somerset West	1990 ± 50	Pta-4411	[4, 5]
	SAM -AP 5041	F	Melkbosstrand	2010 ± 50	Pta-4376	[4, 5]
	SAM -AP 5035b	M	Melkbosstrand	2011 ± 30	OxA-V-2055-46	This study
	SAM -AP 1443	M	Gordon's Bay	2050 ± 50	Pta-2309	[4, 5]
	SAM -AP 1142	M	Falsebay Somerset Strand	2090 ± 27	OxA-V-2056-32	This study
	UCT 220	M	Blouberg Strand	2100 ± 21	Pta-5678	[4]
	SAM -AP 6260a	F	Melkbosstrand	2120 ± 60	Pta-9069	This study
	SAM -AP 4636	M	Blaauwberg Strand	2130 ± 45	Pta-4379	[4, 5]
	SAM -AP 6313b	M	Melkbosstrand	2140 ± 29	OxA-V-2056-47	This study
	SAM -AP 5082	M	Houtbay	2150 ± 60	Pta-4199	[4, 5]
	SAM -AP 6313a	F	Melkbosstrand	2161 ± 30	OxA-V-2055-44	This study
	SAM -AP 1441	M	Melkbosstrand	2170 ± 60	Pta-4201	[4, 5]
	UCT 134	M	Sandy Bay/Llundudno	2210 ± 40	GrA-23226	This study

Table continued:

	SAM -AP 4942	M	Kommetjie	2220 ± 45	Pta-4829	[4, 5]
	UCT 436	F	Langebaan Lagoon	2240 ± 60	Pta-8751	This study
	SAM -AP 4301	F	Noordhoek	2250 ± 30	OxA-V-2055-40	This study
	SAM -AP 4299	F	Noordhoek	2294 ± 29	OxA-V-2065-46	This study
	SAM -AP 6043	M	Melkbosstrand	2295 ± 28	OxA-V-2056-40	This study
	SAM -AP 4300	F	Noordhoek	2304 ± 29	OxA-V-2065-37	This study
	SAM -AP 4899	M	Saldanha	2440 ± 60	Pta-4149	[4, 5]
	SAM -AP 39	F	Gordon's Bay	2448 ± 29	OxA-V-2055-43	This study
	SAM -AP 5070	F	Melkbosstrand	2573 ± 31	OxA-V-2056-46	This study
	SAM -AP 4906a	F	Blouberg Strand	2635 ± 29	OxA-V-2065-35	This study
	SAM -AP 5095	F	Saldanha	2660 ± 70	Pta-4674	[4]
	SAM -AP 4627	F	Darling	2665 ± 27	OxA-V-2056-34	This study
	SAM -AP 4202	F	Kommetjie	2673 ± 29	OxA-V-2056-25	This study
	UCT 167	M	Vlammink Vlei, Velddrif	2695 ± 45	GrA-23222	This study
	NMB 1827	F	Gordon's Bay	2815 ± 40	GrA-23229	This study
	UCT 162	M	Ysterfontein, Darling	2880 ± 50	Pta-929	[4, 5]
	UCT 421	F	Mud River near Darling	2895 ± 45	GrA-23217	This study
	SAM -AP 6147	M	Saldanha	2920 ± 60	Pta-8774	This study
	SAM -AP 6071	M	Vredenberg	2935 ± 32	OxA-V-2055-42	This study
	SAM -AP 6317	M	Melkbosstrand	2970 ± 60	Pta-8807	This study
	SAM -AP 4906b	F	Blouberg Strand	2977 ± 33	OxA-V-2056-48	This study
	UCT 435	F	Langebaan Lagoon	2980 ± 60	Pta-5034	[1]
	UCT 343	F	Simonstown	2985 ± 45	GrA-23221	This study
	SAM -AP 6051	F	Byeneskranskop, Bredasdorp	3190 ± 50	Pta-2969	[6]
	SAM -AP 6319	F	Melkbosstrand	3200 ± 35	Pta-8752	This study
	SAM -AP 6318	M	Melkbosstrand	3310 ± 60	Pta-8741	This study
	SAM -AP 4974	F	Gansbaai	3363 ± 34	OxA-V-2055-48	This study
	SAM -AP 4298	F	Kommetjie	3380 ± 33	OxA-V-2055-41	This study
	UCT 112	M	Darling Sea Coast	4445 ± 50	Pta-2003	[4, 5]
	SAM -AP 6272	M	Darling district	5830 ± 80	Pta-9082	This study
	SAM -AP 4692	M	Peer's Cave, Fish Hoek	*ca.* 12000	no published date	-
Southern Region	**UCT 262**	M	Oakhurst Rock Shelter, Wilderness	510 ± 40	GrA-23221	This study
	NMB 1207	M	Hartenbos, near Mossel Bay	560 ± 50	Pta-8755	This study
	UCT 583	M	Gouritz River, Mossel Bay	560 ± 45	Pta-8760	This study
	UCT 157	M	Ladysmith, Cape Province	587 ± 28	OxA-V-2055-45	This study
	A 1153	F	Steytlerville	636 ± 26	OxA-V-2065-47	This study
	NMB 1219	M	Groot Brak River	650 ± 60	Pta-8804	This study
	NMB 1338	M	Wittedrif, Knysna	650 ± 35	GrA-23711	This study
	UCT 114	M	Cape St. Francis	650 ± 40	GrA-23654	This study
	UCT 83	M	Cape St. Francis	680 ± 40	GrA-23072	This study
	SAM -AP 4180	F	Thysbay, Humansdorp	688 ± 27	OxA-V-2056-23	This study
	UCT 582	F	Gouritz River, Mossel Bay	740 ± 40	Pta-7178	[7]
	A 1154	M	Steytlerville	905 ± 25	OxA-V-2066-33	This study
	UCT 70	M	Ratel River, Bredasdorp	920 ± 40	GrA-23074	This study
	A 1117	F	Lime Bank, Loerie	1060 ± 50	Pta-8727	This study
	SAM -AP 4898	M	Robberg	1084 ± 26	OxA-V-2056-37	This study
	SAM -AP 1260	M	Outshorn	1137 ± 27	OxA-V-2066-28	This study
	ALB 244(1)	F	Paardefontein, near Jansenville	1180 ± 50	Pta-8587	[11]
	UCT 75	F	Cape Agallas, Bredasdorp	1340 ± 40	GrA-23069	This study

Table continued:

	NMB 1707	M	Derbyshire, Plettenberg Bay	1394 ± 24	OxA-V-2064-53	This study
	NMB 5	F	Plettenberg Bay	1423 ± 26	OxA-V-2064-49	This study
	SAM -AP 4874	M	Cape St. Francis	1426 ± 29	OxA-V-2056-45	This study
	SAM -AP 6213	M	Sedgefield, Cape Province	1558 ± 27	OxA-V-2065-39	This study
	UCT 109	M	Humansdorp district	1590 ± 50	GrA-23656	This study
	NMB 83	M	Cape St. Francis	1590 ± 40	GrA-23227	This study
	SAM -AP 4790	F	Hermanus	1610 ± 150	Pta-2163	[1]
	ALB 323	F	Sand River, Cape St Francis	1620 ± 35	Pta-8578	[11]
	SAM -AP 320g	M	Klein Brakriver, Mossel Bay	1707 ± 27	OxA-V-2056-24	This study
	A 1166	M	Humewood, Port Elizabeth	1818 ± 27	OxA-V-2056-33 A	This study
	A 1152	M	Amsterdam Hoek	1850 ± 35	Pta-8757	[11]
	SAM -AP 1473	M	Onrust, Hermanus	1880 ± 60	Pta-8773	This study
	A 1127	F	Jeffrey's Bay	1891 ± 29	OxA-V-2066-36	This study
	UCT 78	F	Cape St. Francis	2145 ± 40	GrA-23241	This study
	SAM -AP 278g	F	Klein Brakriver, Mossel Bay	2158 ± 28	OxA-V-2065-43	This study
	NMB 1203	F	Groot Brak River Cave	2180 ± 50	Pta-8783	[11]
	NMB 1204	F	Groot Brak River	2210 ± 35	Pta-8744	[11]
	SAM -AP 4312	F	Mossel Bay	2260 ± 170	Pta-2164	[1]
	A 1114	M	Knysna	2271 ± 33	OxA-V-2055-51	This study
	UCT 107	M	Knysna	2290 ± 50	Pta-6815	[2]
	SAM -AP 34	M	George, Touwsriver Mouth	2310 ± 25	Pta-6599	[2]
	SAM -AP 1146	M	Robberg, Plettenberg Bay	2321 ± 28	OxA-V-2065-44	This study
	NMB 82	M	Thysbaai, Cape St. Francis	2335 ± 40	GrA-23228	This study
	ALB 222	M	Seal Point, Cape St Francis	2540 ± 60	Pta-8636	[11]
	ALB 301	M	St. Francis Bay	2570 ± 50	Pta-8684	[11]
	SAM -AP 5050	F	Robberg, Plettenberg Bay	2580 ± 60	Pta-7927	[12]
	A 1115	M	Knysna	2588 ± 28	OxA-V-2065-48	This study
	NMB 1639	F	Robberg, Plettenberg Bay	2590 ± 60	Pta-6965	[2]
	SAM -AP 1878b	F	Robberg, Plettenberg Bay	2620 ± 35	Pta-2145	[1]
	NMB 86	F	Cape St. Francis	2705 ± 40	GrA-23657	This study
	SAM -AP 5049	M	Robberg, Plettenberg Bay	2740 ± 50	Pta-7934	[12]
	SAM -AP 5048	M	Robberg, Plettenberg Bay	2780 ± 60	Pta-7924	[12]
	A 1172	F	Witcher's Cave	2950 ± 40	GrA-23647	This study
	NMB 1242	M	Matjesriver, Plettenberg Bay	3030 ± 26	OxA-V-2064-50	This study
	NMB 1273	M	Matjesriver, Plettenberg Bay	3050 ± 60	Pta-6942	[2]
	NMB 1202	M	Groot Brak River, Mossel Bay	3140 ± 50	Pta-8801	[11]
	SAM -AP 1128	F	Robberg, Knysna	3156 ± 33	OxA-V-2055-49	This study
	SAM -AP 1145	M	Robberg, Plettenberg Bay	3210 ± 70	Pta-2284	[1]
	NMB 4	M	Robberg, Plettenberg Bay	3236 ± 33	OxA-V-2064-48	This study
	SAM-AP 1871	F	Robberg, Knysna	3310 ± 60	Pta-2273	[1]
	ALB 354	F	Paradysstrand, Jeffrey's Bay	3340 ± 60	Pta-8680	[11]
	A 1112	F	Zitzikama Caves, Tsitsikama coast	3355 ± 45	GrA-23232	This study
	SAM -AP 1879	M	Robberg, Knysna	3440 ± 60	Pta-2283	[1]
	UCT 161	F	Plettenberg Bay	3451 ± 26	OxA-V-2064-54	This study
	SAM -AP 31	M	Blaauwkrantz	3576 ± 30	OxA-V-2065-34	This study
	SAM -AP 32	M	Humansdorp district	3754 ± 35	OxA-V-2055-47	This study
	NMB 1640	F	Robberg, Plettenberg Bay	4240 ± 70	Pta-8792	This study
	A 1124	M	Port Elizabeth	4320 ± 32	OxA-V-2056-42	This study
	A 1139	F	Kenkelbosch	4800 ± 50	Pta-8816	[11]

Table continued:

	NMB 1275	M	Matjesriver, Plettenberg Bay	4850 ± 60	Pta-6986	[2]
	UCT 180	M	Oakhurst Rock Shelter, Wilderness	6180 ± 70	Pta-3718	[9]
	SAM -AP 4182	M	Drury's Cave, Cold Stream Humans Dorp	6811 ± 36	OxA-V-2056-26	This study
	SAM -AP 5055	M	Robberg, Plettenberg Bay	6995 ± 50	OxA-V-2065-42	This study
	UCT 156	M	Knysna Heads, Knysna	10110 ± 80	GrA-23223	This study
Eastern Region	**A 2226**	M	Willovale Coast, Transkei	800 ± 50	Pta-8728	This study
	A 2227	M	Willovale Coast, Transkei	1150 ± 50	Pta-8819	[11]
	ALB 131	M	Spitzkop farm, Springvale Siding	4700 ± 60	Pta-5979	[10]

Table 6.1: The cranial sample used in this study.
References: **1**, A. G. Morris (1992d); **2**, Sealy and Pfeiffer (2000); **3**, Pfeiffer and Sealy (2005); **4**, Sealy (1989); **5**, Sealy and van der Merwe (1988); **6**, de Villiers and Wilson (1982); **7** Morris *et al.* (in press), **8**, Hausman (1980); **9**, Patrick 1989; **10**, Albany Museum register; **11**, Sealy pers. comm.; **12**, Muller (2002).

region, all crania were derived from burials located between the southern reaches of the Great Karoo and the Indian Ocean.

The cranial sample from the western region consists of 8 crania (2 female, 6 male); that from the south-western region consists of 70 crania (33 female, 37 male); that from the southern region consists of 72 crania (27 female, 45 male); and that from the eastern region consists of 3 crania (3 male). Burial context varies throughout the research region. Crania from the western and south-western regions are primarily from isolated burials in dune sands, with no or very little associated cultural material. On the other hand, many crania from the southern region are from burials in rock shelters that have yielded multiple skeletons in better defined cultural contexts. In the eastern region, crania are derived from inland cave and coastal dune field context. All crania are from the collections of five South African institutions. These are Iziko: South African Museum, Cape Town (prefix: **SAM-AP**) (83 crania); the Department of Human Biology,

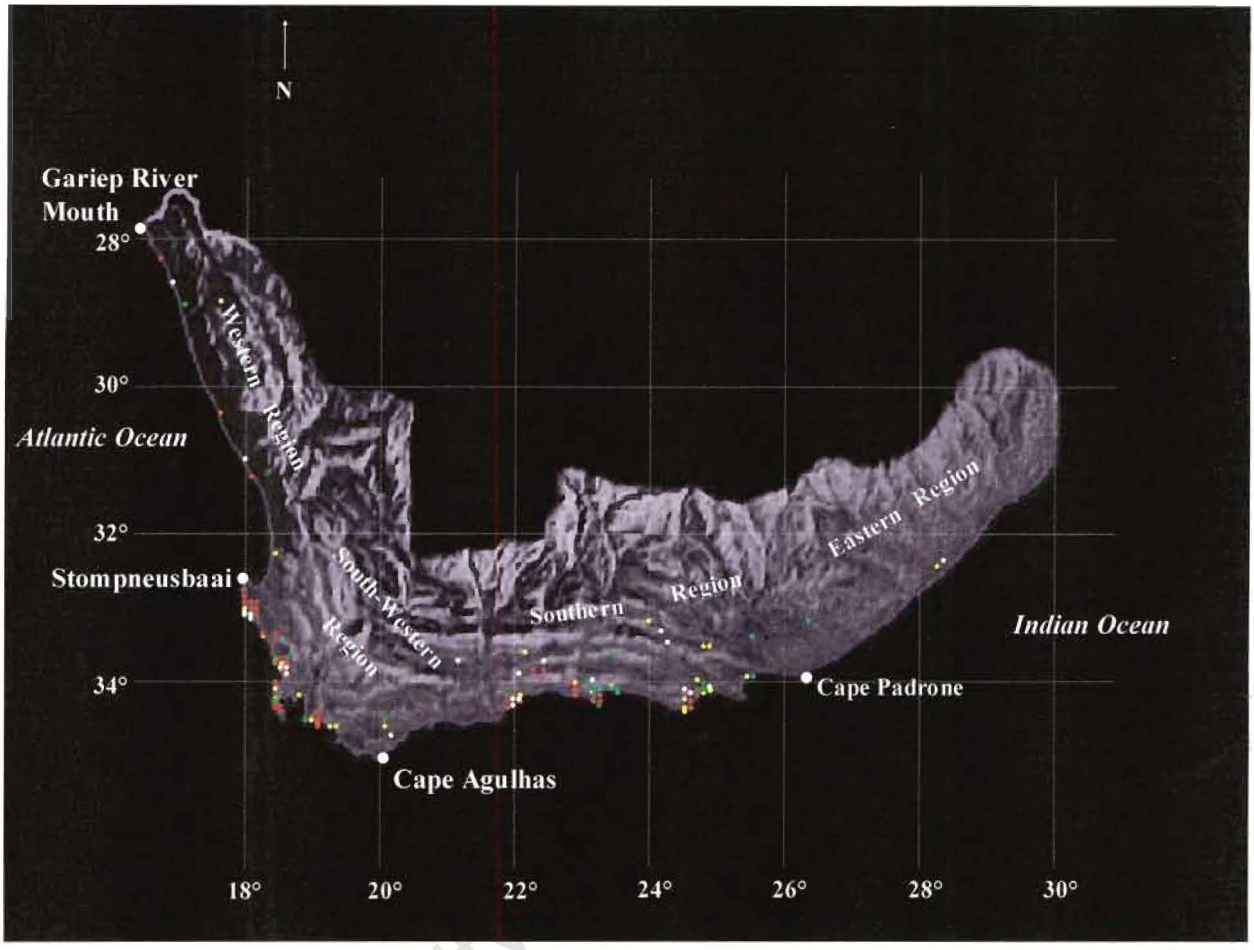

Figure 6.1: The geographic and temporal distribution (colour-coded) of crania used in this study.

1000 BP – 500 BP
2000 BP - 1000 BP
3000 BP - 2000 BP
4000 BP - 3000 BP
5000 BP - 4000 BP
6000 BP - 5000 BP
7000 BP - 6000 BP
11 000 BP - 10 000 BP
ca. 12 000 BP

University of Cape Town, Cape Town (prefix: **UCT**) (32 crania); the Albany Museum, Grahamstown (prefix: **ALB**) (6 crania); the National Museum, Bloemfontein (prefix:

NMB) (18 crania); and the Department of Anatomy, University of the Witwatersrand, Johannesburg (**A**) (14 crania).

Museum catalogues were consulted for information on the geographic locations of graves, burial styles and cultural associations. The sex and age of each individual was independently assessed using the criteria suggested in Buikstra and Ubelaker (1994). When postcranial indicators of sex were available, morphological indicators from both the cranium and pelvis were used. Otherwise, sex was ascertained on the cranium alone.

DATING

All crania measured in this study, except one (SAM-AP 4692, from Peers Cave near Cape Town), have been securely radiocarbon (^{14}C) dated, many specifically for this study. As mentioned in Chapter 4, a date has been obtained on post-cranial bone from SAM-AP 4692, but has not been published, and is not available for citation. However, reliable sources report that it is *ca.* 12 000 BP.

As discussed in Chapter 3, poor dating of the Khoesan skeletal record has hindered previous attempts at interpreting patterns of craniofacial variation. Archaeological research has demonstrated that not only was there frequent changes in technology, mobility, diet and settlement patterns during the Holocene, but two new life ways, namely herding and farming, were introduced. Since there is little doubt that these factors would have influenced the biological character of human populations in the region, it is imperative that any new study be performed on a fully dated cranial sample. Only then is one in a position to link patterns of craniofacial variation to a probable cause.

Past studies have often employed cultural and burial context as a guide to the likely age of human remains (e.g. Dreyer and Meiring 1937). This practice has, however, proved to be notoriously problematic (A. G. Morris 1984, 1992c; Inskeep 1986). Even at sites where human remains are found in well-defined cultural contexts, burials and archaeological deposits often span several time periods, making it difficult to link the two (Koningsberg 1990). In South Africa, few prehistoric human skeletons have been securely dated on cultural context alone. In the cases that this was possible, skeletons were usually from relatively recent excavations where excavators had followed modern archaeological practices. Unfortunately, the majority of human skeletons in collections around the country were collected during the first half of the twentieth century when excavators rarely kept detailed accounts of their excavations. Since few of these early skeletons have adequate descriptions of their burial style and cultural context, the only way to provide a secure chronological context is to date them directly.

At the start of this research, only 47 crania complying with the selection criteria as set out above had associated radiocarbon dates. Since a much larger sample was required for my study, a dating programme was initiated. This resulted in 20 regular radiocarbon (^{14}C) dates and 74 Accelerator Mass Spectrometry (AMS) dates being added to the original tally. An additional 12 dates were provided by separate projects (Pfeiffer and Sealy 2006; Sealy pers. comm.).

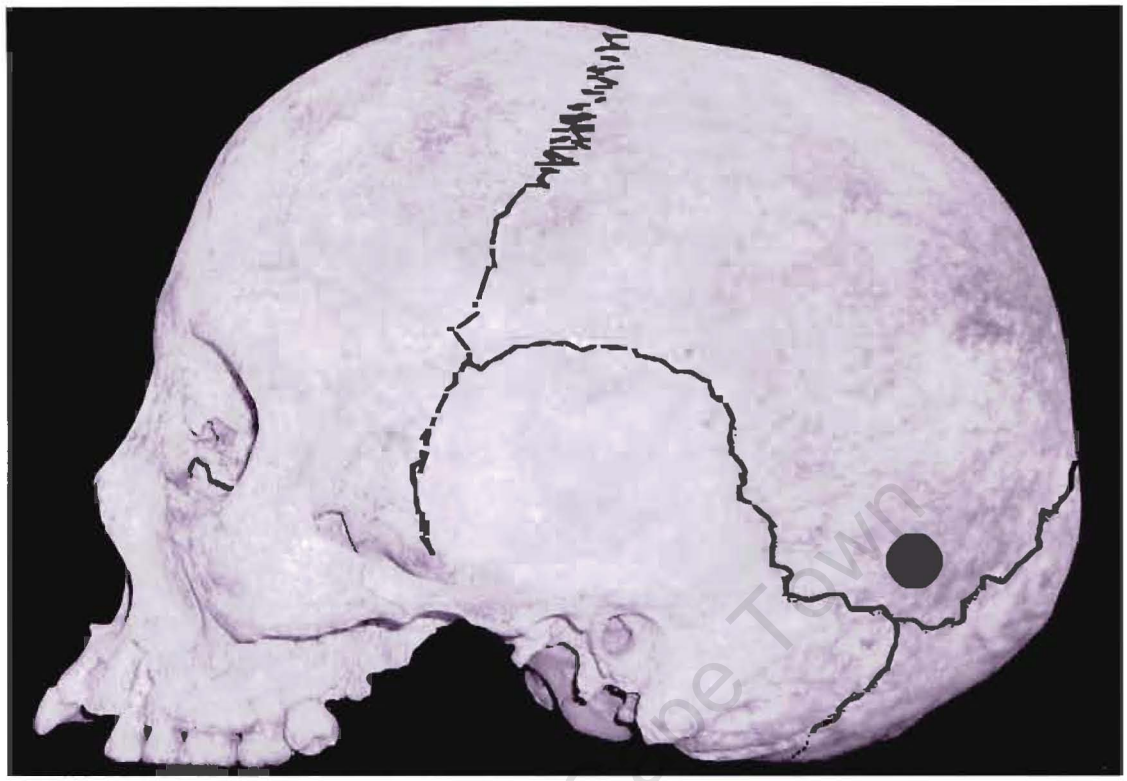

Figure 6.2: Location of the bone sample taken for AMS analysis.

Two methods of dating were employed. When a skeleton was complete or near complete, samples of bone were taken for conventional ^{14}C analysis, usually from one side of the rib cage and/or from a fibula. These elements were chosen as they are least informative in morphological studies. Whenever possible, broken elements were sampled in preference to complete ones. Where very little of the postcranial skeleton was present, or only a cranium existed, samples were taken for AMS analysis. Small plugs of bone (approximately 10 -15 mm in cross-section) were drilled using a hollow bit from the undiagnostic parietal region just above asterion (Figure 6.2). Samples for conventional ^{14}C and AMS analyses were sent to the Quaternary Dating Research Unit (QUADRU), at the Council for Scientific and Industrial Research (CSIR) in Pretoria, South Africa. Bone collagen was extracted at QUADRU, and conventional ^{14}C dates determined there.

Collagen for AMS dating was sent to the CIO Accelerator Laboratory in Gröningen, Holland, where the AMS dates were generated. Samples for which very thorough pre-treatment was considered important were sent to the Radiocarbon Unit of the Research Laboratory for Archaeology at Oxford University. These included samples from crania thought to have been treated with varnish, glue or other consolidants. For these samples, I extracted acid-insoluble bone protein in the Department of Archaeology at the University of Cape Town. Further purification and isolation of amino acids was carried out in the laboratory at Oxford, according to the usual protocol. Dates were obtained for the amino acid fraction.

Dates for all the specimens analysed in this study are presented in Table 6.1. The prefix in the laboratory number identifies the laboratory of origin for each date. These are as follows: Quaternary Dating Research Unit, Pretoria, South Africa (**Pta-**); Geochron Laboratories, Massachusetts, USA (**Gx-**); CIO Accelerator Laboratory, Gröningen, Holland (**GrA-**); and the Radiocarbon Unit of the Research Laboratory for Archaeology and the History of Art, Oxford University, Great Britain (**OxA-**). Following Sealy and Pfeiffer (2000) and Mitchell (2002), dates were left uncalibrated for consistency with other discussions of the LSA of South Africa (e.g. H. J. Deacon and J. Deacon 1999).

DATA CAPTURE

In traditional multivariate studies of biological form, an object's form is characteristically captured as a set of linear distances and/or angles using a variety of hand-held measuring devices such as callipers. In order to facilitate comparison between samples, measurements are often standardised, and follow one or other measurement protocol. For

instance, many recent studies of human craniofacial variation employ the set of measurements used by Howells (1973, 1989) in his world-wide survey of human craniofacial variation (e.g. J. F. Powell and Neves 1999; Owsley and Jantz 1999; González-José *et al.* 2005; Neves and Hubbe 2005) . At face value, the use of traditional methods of data collection appears to allow access to a large comparative sample (i.e. Howells' database) to which researchers can compare their study sample. In reality though, there are several fundamental problems associated with traditional measurements. Firstly, measurements may not necessarily be comparable between specimens, let alone between samples. For instance, maximum cranial breadth and maximum frontal breadth, two common measurements in traditional multivariate studies (Howells 1973, 1989), are subjective and often difficult to determine. Repeatability of these kinds of measurements is often low within studies. The problem becomes even more acute when data from more than one researcher are analysed. According to Richtsmeier *et al.* (2002), a second problem associated with data collected in the traditional manner, is that measurements normally represent a series of unrelated variables that do not reflect the geometry of the object as a whole. It is thus difficult to investigate co-variation between various regions. For instance Wescott and Jantz (2005) note that data collected using traditional methods were able to show that there was a secular trend in the vault heights of black and white Americans over the last 150 years. However, studies based on these traditional measurements were unable to determine whether this was due to alterations in the inferior or superior vault. Thirdly, traditional measurements often have very little biological basis (e.g. maximum cranial breadth). Instead, Richtsmeier *et al.* (1992) note that traditional measurements are often chosen on

an a priori basis and represent those measurements that are thought to best distinguish between forms. This makes it difficult to investigate issues related to phylogeny, development, biomechanics or evolution.

The need to accurately capture the often complex shapes of biological objects has seen scientists increasingly turn to the field of geometric morphometrics in the last couple of years. Geometric morphometrics, which has been described as a combination of the fields of geometry and biology by Bookstein (1982), preserves the integrity of an object by capturing its form as a series of 2 or 3 dimensional coordinates of predetermined landmarks. Whereas traditional data collection methods depend on measuring devices aimed at recording linear or angular measurements, the capture of landmark coordinates is facilitated by surface imaging devices such as single point landmark digitizers, video capture devices, stereophotogrammetry and tomographic imagers. The landmark coordinates, once captured, represent the raw data that may then be used in further analyses to investigate a biological question. For instance, landmark coordinates may be transformed into points in the shape space of Kendall (1994), where for each object, the transformed coordinates represent a single point in shape space (Goodall 1991; Rohlf 1999). Landmark data may also be transformed into a matrix of linear distances between all possible landmarks (Ackermann 1998). Once landmark coordinates have been transformed, they may be investigated by any number of traditional multivariate statistical methods such as Principal Components Analyses (PCA).

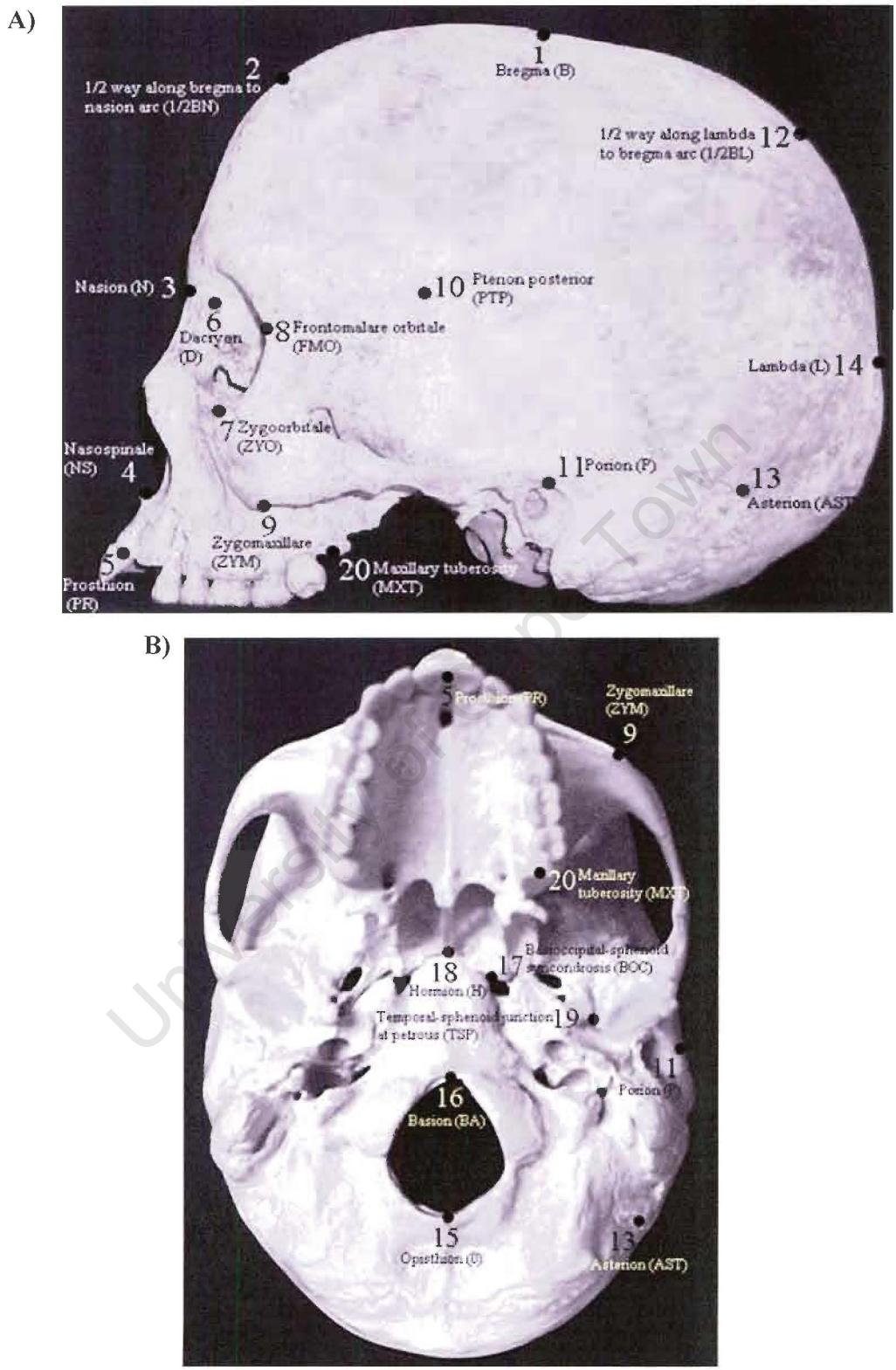

Figure 6.3: The locations of landmarks used in this study. A) Lateral view; B) Inferior view.

Capturing the form of a biological object as a series of 2 or 3 dimensional coordinates has several advantages over traditional methods of data collection. Firstly, unlike many traditional measurements, landmarks are normally precise locations on biological objects (e.g. suture intersections). Since the precise locations of most landmarks normally used in geometric morphometric studies are easy to define and unambiguous, repeatability of landmarks are normally very high. This makes comparison with data collected by other researchers unproblematic and more useful for future reference (Hildebolt and Vannier 1988; Cheverud *et al.* 1992; Ackermann 1998). Secondly, landmarks normally also have some developmental, functional, structural or evolutionary significance (Richtsmeier *et al.* 2002). Data collected in this manner can thus be used to answer questions about complex biological processes. Thirdly, unlike traditional measurements which collapse an object into a series of unrelated linear or angular measures, landmarks are recorded relative to one another in 2 or 3 dimensional space. As such, it is possible to investigate changes in one landmark relative to other landmarks (Richtsmeier *et al.* 2002; Wescott and Jantz 2005). Fourthly, this method of data collection is accurate and fast. It is thus possible to digitize large collections with great accuracy in a short time period. Based on the advantages associated with using landmark data, this method of data collection is the preferred method in this study.

Three-dimensional coordinates (3-D) of twenty cranial landmarks were recorded on the left side of the cranium (Figure 6.3 and Table 6.2) using a Microscribe™ 3-D digitizer and *InScribe-32* software (Immersion Corp., San Jose, CA, USA). Unlike traditional methods of data collection where some linear distances (e.g. maximum length and

maximum breadth) do not require homologous landmarks (i.e. when the same landmark can be accurately reproduced between objects), the identification of such landmarks is a requirement before digitizing can commence. Bookstein (1991) defined several levels of homology. Homology type I concerns discrete juxtapositions of tissues (points in space where two or three structures meet, such as cranial sutures) and have the highest rates of

Landmark #	Landmark	Landmark Description
1	**B**	Bregma
2	**1/2BN**	Halfway along Bregma to Nasion arc
3	**N**	Nasion
4	**NS**	Nasospinale
5	**PR**	Prosthion
6	**D**	Dacryon
7	**ZYO**	Zygoorbitale
8	**FMO**	Frontomalare orbitale
9	**ZYM**	Zygomaxillare
10	**PTP**	Pterion posterior
11	**P**	Porion
12	**1/2BL**	Halfway along Lambda to Bregma arc
13	**AST**	Asterion
14	**L**	Lambda
15	**O**	Opisthion
16	**BA**	Basion
17	**BOC**	Basioccipital-sphenoid syncondrosis
18	**H**	Hormion
19	**TSP**	Temporal-sphenoid junction at petrous
20	**MXT**	Maxillary tuberosity

Table 6.2: Cranial landmarks used in this study and their descriptions.

reproducibility. Homology type II concerns maxima of curvatures of morphogenetic processes (e.g. the glabella). Homology type III concerns constructed landmarks (e.g. midpoints between two landmarks). In this study fourteen landmarks (B, N, NS, PR, D, ZYO, FMO, ZYM, PTP, AST, L, BOC, H, TSP) are type I according to the criteria of Bookstein (1991), four are type II (P, O, BA, MXT) and two are type III (1/2BN, 1/2BL).

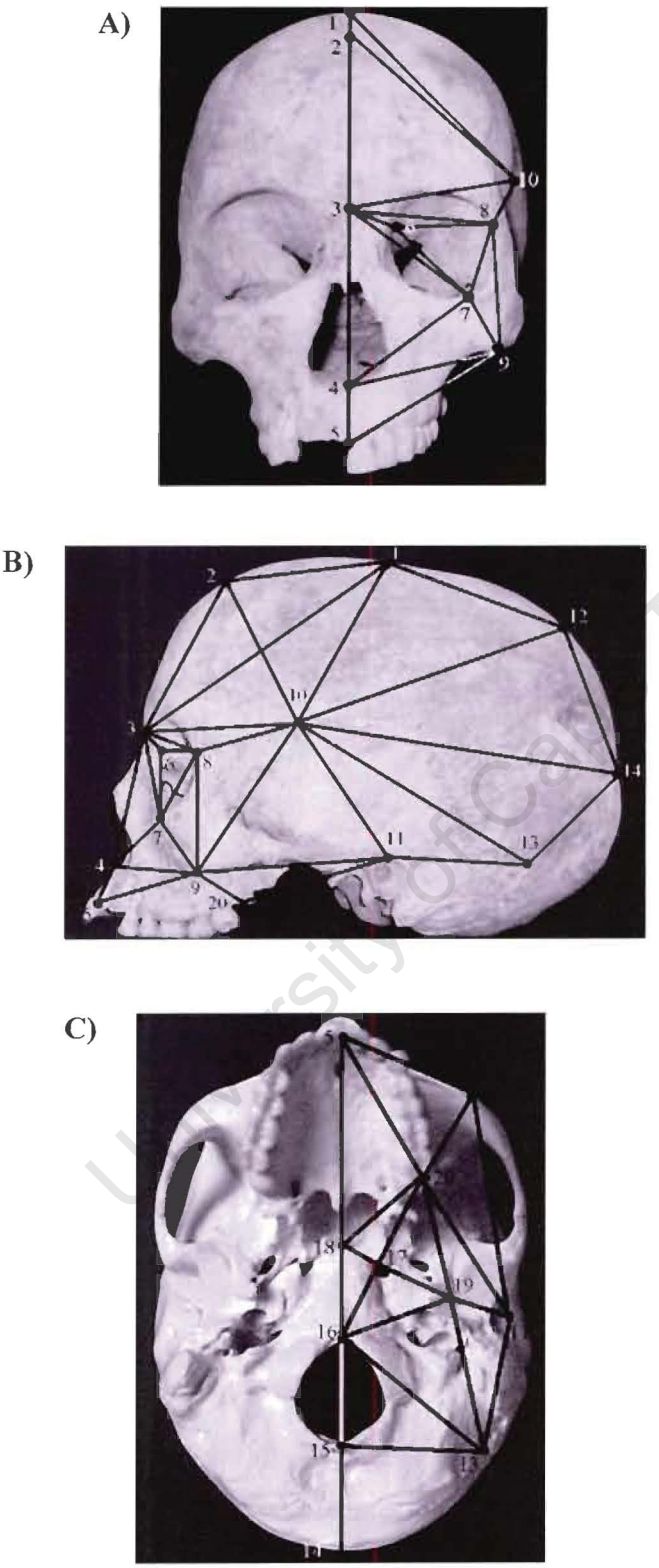

Figure 6.4: The subset of 48 distance variables used in this study. A) Anterior view; B) Lateral view; C) Inferior view.

1-2	B-1/2BN
1-3	B-N
1-10	B-PTP
1-12	B-1/2BL
2-3	1/2BN-N
2-10	1/2BN-PTP
3-4	N-NS
3-6	N-D
3-7	N-ZYO
3-8	N-FMO
3-10	N-PTP
4-5	NS-PR
4-3	NS-ZYO
4-9	NS-ZYM
5-9	PR-ZYM
5-18	PR-H
5-20	PR-MXT
6-7	D-ZYO
6-8	D-FMO
7-8	ZYO-FMO
7-9	ZYO-ZYM
8-9	FMO-ZYM
8-10	FMO-PTP
9-10	ZYM-PTP
9-11	ZYM-P
9-20	ZYM-MXT
10-11	PTP-P
10-12	PTP-1/2BL
10-13	PTP-AST
10-14	PTP-L
11-13	P-AST
11-19	P-TSP
11-20	P-MXT
12-14	1/2BL-L
13-14	AST-L
13-15	AST-O
13-16	AST-BA
13-19	AST-TSP
14-15	L-O

Table continued:

15-16	**O-BA**
16-17	**BA-BOC**
16-18	**BA-H**
16-19	**BA-TSP**
17-18	**BOC-H**
17-19	**BOC-TSP**
17-20	**BOC-MXT**
18-20	**H-MXT**
19-20	**TSP-MXT**

Table 6.3: Subset of variables selected for further analyses.

Ten landmarks are located on the sagittal plane (B, 1/2BN, N, NS, PR, 1/2BL, L, O, BA, H) and ten on the left side of the cranium (D, ZYO, FMO, ZYM, PTP, P, AST, BOC, TSP, MXT). Crania were mounted in such a way that access could be gained to all twenty landmarks without having to reset the cranium. Landmarks were then digitized in numeric order from one to twenty for all crania.

GENERATING LINEAR DISTANCES FROM COORDINATE DATA

The statistical methods employed in the evaluation of the hypotheses set out in Chapter 5 require both coordinate data and linear distances between landmarks. In Euclidean 3-D space, the distance between landmark (x_1, y_1, z_1) and (x_2, y_2, z_2) is given by the Pythagorean Theorem:

$$d = \sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2 + (z_2 - z_1)^2}$$

Solving this equation would give the Euclidean distance between two landmarks. Distances were calculated between all 20 landmarks, resulting in 190 variables for each cranium in the study sample. The data set of 190 variables contains a high percentage of redundant variables, i.e. more than one variable measures the same morphological region.

Its large size also complicates analyses. Therefore, a subset of 48 variables was selected for further analysis (Figure 6.4 and Table 6.3). Care was taken to choose at least one variable that would cover all major regions of the cranium completely. This approach provided an accurate representation of form without redundancy.

VARIABLE REPEATABILITY

Variable repeatability (of the distance data) was used to gauge the accuracy with which data was captured. As per Cheverud (1995) and Ackermann (1998, 2002), repeatability is the proportion of the total variance due to individual differences, in contrast to variation due to measurement error. Thirty crania were randomly chosen to test the repeatability of measurements. The equation to calculate repeatability is $t = V_b/(V_b+V_w)$, where V_b is the variance between samples and V_w is the variance within samples. V_b is calculated as $V_b=(MS_b-MS_w)/n$, where MS_b is the mean-square between samples, MS_w the mean-square within samples and n the number of repeats. V_w is equal to MS_w. In this study each cranium was measured three times, thus n= 3. The repeatability of the 20 landmarks was also evaluated via the same method. To achieve this, each landmark had to be represented by a linear distance. Coordinate data from the three repeats on each of the 30 crania used in the repeatability test were first subjected to Procrustes analysis. Then the coordinates from individual specimens were used to calculate the Euclidean distance of each landmark to the common centroid. This yielded 60 linear distances, one per landmark for each of the three repeats from which repeatability was estimated.

DATA ANALYSIS

Limitations associated with the early human fossil record make analyses of early cranial samples quite tricky. Problems associated with small sample sizes are ubiquitous in any physical anthropological study focussing on prehistoric human skeletal material. Analyses are further compounded by the often fragmentary nature of many skeletal samples. Investigations into the origins of recent patterns of human craniofacial variation are no different. These problems are particularly acute for the pre-Holocene period. Because of the fragmentary nature of the skeletal record for this period, researchers often have to rely on comparisons between temporally and geographically diverse cranial samples to determine past patterns of craniofacial variation. Reliance on such diverse samples complicates the determination of past levels of craniofacial diversity in prehistoric populations. For instance, such samples rarely represent a biological population. The limited prehistoric remains available for study also do not provide a complete picture of past levels of variation.

Jantz and Owsley (2001) have divided the current approaches used to analyse Pleistocene/early Holocene crania into three broad groups: (1) crania from similar time periods are pooled and compared as a temporally bounded sample to other populations; (2) individual early crania are compared to recent samples; (3) fossil crania are compared to one another using a covariance matrix from a large sample of recent crania.

Jantz and Owsley (2001) do not favour pooling early cranial samples. In modern populations where the patterns of variation within biological populations are well-defined, pooling is acceptable. In the case of early crania, though, we do not know how

homogenous populations actually were, nor are we certain that individuals are actually from the same populations. If prehistoric crania are derived from populations characterised by substantial metric differences, as may have been the case in many Pleistocene and early Holocene populations, or were derived from separate populations, pooling could produce an unrealistic average configuration not representative of past patterns of variation (Jantz and Owsley 2001).

A commonly used approach is to compare the crania of early populations to those of recent populations (contemporary/historic/late prehistoric) (Owsley and Jantz 1999; J. F. Powell and Neves 1999; Jantz and Owsley 2001). This is routinely accomplished using typicality probabilities (Albrecht 1992). With this approach, Mahalanobis' D^2 distances (Mahalanobis 1936) are calculated between individual early crania and a number of recent comparative groups. Early crania are then assigned to the recent group to which they display the closest morphological similarity. Although Jantz and Owsley (2001) have suggested that this approach is useful for speculating on historical links between fossils and extant populations, this approach has been criticised by others. According to Swedlund and Anderson (2003), the temporal separation that normally exists between early and recent crania is normally so great that, even if morphological similarities can be identified between early crania and those of recent populations, similarities mean very little in terms of actual relatedness. This is because this approach ignores the effects of evolutionary forces and environmental plasticity on cranial form, either of which could have affected the ancient specimens and/or the modern reference samples in unknown ways.

The third approach, which allows early crania to be compared to one another using an appropriate covariance matrix, has been the most successful approach to date. In this approach, Mahalanobis distances (D) are calculated between early crania. This approach takes cognisance of individual variation between crania by treating each as an individual (Van Vark 1990; Van Vark and Schaafsma 1992; Van Vark *et al.* 1992; Jantz and Owsley 2001; Owsley and Jantz 1999; J. F. Powell and Neves 1999; Cunningham and Wescott 2002). Via this approach, it is possible to investigate morphological differences between crania, investigate levels of homogeneity and heterogeneity within samples, and identify populations and sub-populations based on morphological similarities.

The methods employed in this thesis follow the third approach closely. In addition to investigating morphological links between individual crania (Malahanobis D), similarities and differences in craniofacial form between individual crania are also examined (Principal components analyses). Trends in craniofacial shape and size are investigated for individual specimens (Generalized Procrustes Analysis). The following sections discuss the methods used in the thesis in more depth.

TRADITIONAL MULTIVARIATE STATISTICAL METHODS

MAHALANOBIS' GENERALISED DISTANCE (D^2) ANALYSIS

Mahalanobis' generalised distance (D^2) was used to determine morphological distances between crania, identify possible populations and outliers, and measure levels of homogeneity and heterogeneity in samples. This method has been widely and successfully employed in the analysis of prehistoric human craniofacial variation

(Mahalanobis 1936; Van Vark 1990; Van Vark and Schaafsma 1992 Van Vark *et al.* 1992; Jantz and Owsley 2001; Owsley and Jantz 1999; J. F. Powell and Neves 1999; Cunningham and Wescott 2002). Mahalanobis' D^2 distances may be measured between sample means or individual crania. Because Mahalanobis' D^2 distances are dissimilarities, the greater the Mahalanobis' D^2 distance between two samples or crania, the greater the morphological distance. Mahalanobis' D^2 distances are ideal for investigating morphological distances between crania of unknown affiliation because inter-individual comparisons are made using information on the variance covariance structure of an appropriate population, which could be a prehistoric population (Manly 1986). Any differences or similarities between individual crania thus have greater significance because comparisons are made in the context of the morphological variation present in an entire population.

Mahalanobis' D^2 distances between individual crania were calculated in the student's version of the program Mathematica™. The Mahalanobis' Generalised Distance (D^2) equation for distances between groups takes the form

(1) $$D^2_{ij}=(x_i-x_j)'P_w^{-1}(x_i-x_j)$$

where x_i is the vector of t trait means for sample i, x_j is a vector of t trait means for sample j, and P_w^{-1} is the inverse of the pooled within-groups phenotypic covariance matrix for the t traits (Mahalanobis 1936). For inter-individual distances, this equation is altered to

(2) $$D^2_{1,2}=(x_1-x_2)'P_w^{-1}(x_1-x_2)$$

where x_1 and x_2 are the vector of values for individuals 1 and 2 and $\mathbf{P}_w^{-1}$ is the inverse of an appropriate covariance matrix (Van Vark and Schaafsma 1992).

Jantz and Owsley (2001) note that in the case of fossil human populations, the question of what constitutes an appropriate covariance matrix may be tricky. This is because the patterns of variation within extinct populations are largely unknown (Ackermann 1998, 2002, 2003). The ideal scenario would be if the covariance matrix reflects variation within groups with a genetic structure similar to that of populations from which fossil crania are derived (Jantz and Owsley 2001). Since fossils are rare, samples usually do not represent the full range of variation that was once present. An option that many authors take is to use the pooled within–group covariance matrix derived from recent populations (Van Vark and Schaafsma 1992; J. F. Powell and Neves 1999; Jantz and Owsley 2001; Cunningham and Wescott 2002). This is not an ideal solution, as some populations are known to have undergone temporal change in craniofacial morphology (see Chapter 2). In addition, modern populations may be more homogenous in craniofacial morphology than past populations (Sarich 1997; Jantz and Owsley 2001; Cunningham and Wescott 2002). The approach followed in this thesis, was to use a covariance matrix calculated directly from the 153 crania which make up the study sample. Not only does this sample far exceed the 100 individuals which Ackermann and Cheverud (2002) consider as a robust number from which to calculate a covariance matrix, but its temporal and geographic span provides a reasonable approximation of prehistoric coastal Khoesan population variation.

To make my results comparable with those of other studies investigating the origins of recent human craniofacial morphology (e.g. Jantz and Owsley 2001; Cunningham and Wescott 2002), Mahalanobis' D^2 distances were transformed into Mahalanobis distances ($\sqrt{D^2}$). Inter-individual distances between crania are normally presented as a triangular matrix. However, the sheer number of individual comparisons dealt with in this study, makes this method of evaluating morphological distances between crania impractical. A degree of data reduction was thus required. Levels of homogeneity and heterogeneity within and between cranial samples were investigated by way of medians, means and standard deviations of (D) distances. Medians, means and standard deviations of distances between individual crania and all other crania were also investigated. This provided a quantitative method by which morphological outliers could be identified if present.

Inter-individual distances between crania were also investigated using Principal Coordinates Analysis (PCO) (Gower 1966, 1997; Owsley and Jantz 1999; Jantz and Owsley 2001). All analyses were performed in the program PAlaeontological STatistics (PAST) version 1.37. This method searches for similarities between cases. Also known as Metric Multidimensional Scaling, PCO finds the eigenvalues and eigenvectors of a matrix containing the distances between all data points in a sample. A PCO helps to clarify the structure of a distance matrix. It may do this by expressing the distance matrix in Euclidean space, preserving the relative distances between objects. The closer objects are to one another, the more similar they are. This method thus allows one to visualise distances between individual objects (in this case morphological distances between

crania), and is useful for analysing large amounts of distances. In this study, PCO are preformed on distance values using the Euclidean index.

To determine the significance of distances between individual crania, the criteria established by Defrise-Gussenhoven (1967) was employed. This approach is widely employed by other investigations of craniofacial variation in Pleistocene/Holocene populations (J. F. Powell and Neves 1999; Jantz and Owsley 2001; Cunningham and Wescott 2002; Kidder and Durband 2004). Defrise-Gussenhoven (1967) demonstrated that the $\sqrt{D^2}$ between individuals drawn at random from the same biological population will be distributed as $\sqrt{2t-1}$, where t is the number of dimensions (variables) and with a variance of 1. In the context of this study with t = 48 variables, the test statistic is $\sqrt{2(48)-1} = 9.75$. Distances greater than 1.65 standard deviations above this value (D =11.40) are significant at the 0.05 level (Jantz and Owsley 2001). Based on recent levels of craniofacial variation then, these values are considered to be too large to represent individuals from the same population.

PRINCIPAL COMPONENTS ANALYSIS

Principal Components Analysis (PCA) (Jolife 1986; Dunteman 1989) was employed to further investigate morphological relationships between individual crania, as well as between subsets of crania. This procedure also allows for the identification of the primary morphological differences between individual crania and/or subsets of crania. All analyses were carried out on untransformed (raw) data. Analyses were performed in Systat 11.0™. The computation of the principal components (PCs) was done via the

correlation matrix. As in the calculation of Mahalanobis distances, this method does not require that populations be identified prior to analysis. It has the advantage of being able to reduce a large dataset of (possibly) correlated variables into a (smaller) number of uncorrelated variables, the PCs. Analysing the PCs makes it easier to identify meaningful underlying variables that distinguish crania from each other. PCs may be plotted against each other to visualise morphological relationships in 2 or 3 dimensions. Specimens that are morphologically similar occupy similar multivariate space.

To determine the significance of population effects along components, analysis of variance (ANOVA) (Scheffé 1959; Lindman 1974) was performed using SPSS 13.0 on all PCs with eigenvalues greater than 1. Significant PCs were then plotted to visualise morphological relationships. This method was only applied in the evaluation of Hypothesis 3, where samples sizes were large enough for results to be statistically significant. When evaluating morphological variation in the pre-5000 BP cranial sample, sample size was too small for the application of an ANOVA. In this case the first three PCs which represented most of the variation were evaluated.

GEOMETRIC MORPHOMETRIC ANALYSES

GENERALISED PROCRUSTES ANALYSIS (GPA)

Size and size-related shape (allometry) variables, generated by means of a Generalized Procrustes Analysis (GPA) of landmark coordinates, were used to investigate size and size-related shape change through time (Penin *et al.*. 2002; Berge and Penin 2004; Singleton 2002). GPA is one of several geometric morphometric techniques that may be

used to standardise landmark coordinate data to facilitate morphological studies of biological forms. Coordinate data from several specimens are superimposed in a common (though arbitrary) coordinate system using least-squares estimates for translation and rotation parameters. In so doing, GPA removes variation in digitizing location, orientation and scale. GPA was preferred in this study because it provided size and allometry values for each cranium in the study sample.

Landmark data were standardised using APS software version 2.41. After superimposition, the size variable for each cranium (centroid size) was extracted and kept for future analysis. To generate variables that represented shape only, all configurations were scaled to a common unit size, by dividing by centroid size (Bookstein 1986). Configurations were then optimally rotated to minimise the squared differences between corresponding landmarks (Rohlf and Slice 1990). At this stage, the transformed coordinates of each cranium represented points in shape space. A mean shape was defined along with the set of points (individual crania) that clustered around it in shape space. Each mean shape was defined by a set of 3-D coordinates. Each individual cranium now also had a new set of 3-D coordinates defining its position relative to the mean shape. For each landmark, a Procrustes residual is the difference between the position of an individual specimen's landmark and the position of the homologous landmark of the mean shape. Procrustes residuals were calculated for each landmark of all specimens within the study, generating a matrix of Procrustes residuals. The matrix of Procrustes residuals represent the raw data used for any further statistical procedures such as PCA. As per Penin *et al.* (2002), principal components of shape (PCS) were calculated

from a principal components analysis of a variance-covariance matrix of Procrustes residuals. Projection of the Procrustes residuals onto the PCS provides PCS scores which were used to calculate allometric values for each cranium (discussed below).

As per Singleton (2002), the centroid size of each cranium was used to investigate size change in the sample. Defined as the square root of the sum of squared distances of a set of landmarks from their centroid, centroid size was the preferred size metric for this study because it is uncorrelated with any shape variables and purely represents size (Slice *et al.* 1996).

According to Penin *et al.* (2002), allometry as originally set out (Huxley 1932; Teissier 1948), was the comparison of two body dimensions, and does not aim to disassociate size and shape. In this study though, allometry was used in the sense of Gould (1966), Mosimann (1970) and Bookstein (1989, 1991), where allometry is shape change that is related to an increase in size. Following Penin *et al.* (2002) and Berge and Penin (2004), an allometry value for each cranium was calculated using a multivariate regression in which the independent variable was size (centroid size), and the dependent variables, PCS scores calculated from Procrustes residuals. In this study enough PCS scores were included in each analysis to account for more than 90% of shape variance. The significance of this relationship was then tested using an F test of significance. The resulting variable of this multivariate regression is called the "common allometric shape vector" (Penin *et al.* 2002). Points along this vector were plotted against radiocarbon date to visualise the magnitude of size related shape change through time.

EVALUATION OF HYPOTHESES

- Evaluation of Sub-hypothesis 1a: To test whether there were any significant morphological differences between the 6 male crania in the pre-5000 BP sample, inter-individual Mahalanobis distances were calculated between all crania in the sample. Levels of significance between all inter-individual distances were tested using the Defrise-Gussenhoven criteria (1967). Relationships between fossils were visualised in a PCO plot.
- Evaluation of Sub-hypothesis 1b: To test whether pre-5000 BP crania fell within the range of morphological variation of 5000 – 2000 BP populations, inter-individual distances were calculated between the 6 crania in the pre-5000 BP sample and all male crania in the 5000 – 2000 BP sample. The pre-2000 BP comparative sample was chosen to represent the morphology of later Khoesan populations because the post-2000 BP sample may contain immigrants or individuals of mixed ancestry which would obscure results. Levels of significance between all inter-individual distances were tested using the Defrise-Gussenhoven criteria (1967). Medians, means and standard deviations of inter-individual distances were calculated. Relationships between the 6 pre-5000 BP fossils and later males were investigated via a PCO of inter-individual distances. The major morphological differences between crania in the pre-5000 BP sample and those in the 5000 – 2000 BP sample were investigated via PCA.
- Evaluation of Sub-hypothesis 2a: To test whether male cranial size was at its lowest between 4000 and 3000 BP, 3-D coordinates from male crania (12 000-500 BP and 4000-500 BP) were subjected to Procrustes analysis. The resulting

size variables (centroid size) were extracted and plotted against radiocarbon date. Temporal trends in median and standard deviation values of centroid size were also investigated.

- Evaluation of Sub-hypothesis 2b: To test whether female cranial size was at its lowest between 4000 and 3000 BP, 3-D coordinates from female crania (5000-500 BP and 4000-500 BP) were subjected to Procrustes analysis. The resulting size variables (centroid size) were extracted and plotted against radiocarbon date. Temporal trends in median and standard deviation values of centroid size were also investigated.
- Evaluation of Sub-hypothesis 3a: To investigate whether there had been an increase in inter-individual variation in the male sample after 2000 BP, mean and standard deviation inter-individual distance values were calculated separately for pre-2000 BP (5000-2000 BP) and post-2000 BP (2000-500 BP) samples, and compared. In order to be able to identify any morphologically distinct crania, median, mean and standard deviation distance values were also calculated for individual cranium in either period. Similarities between pre-2000 and post-2000 BP crania were investigated via a PCO of inter-individual distances.
- Evaluation of Sub-hypothesis 3b: To investigate whether there had been an increase in inter-individual variation in the female sample after 2000 BP, mean and standard deviation inter-individual distance values were calculated separately for pre-2000 BP (5000-2000 BP) and post-2000 BP (2000-500 BP) samples, and compared. In order to be able to identify any morphologically distinct crania, median, mean and standard deviation distance values were also calculated for

individual cranium in either period. Similarities between pre-2000 and post-2000 BP crania were investigated via a PCO of inter-individual distances.

- Evaluation of Sub-hypothesis 3c: Form differences between pre-2000 BP and post-2000 BP male samples were investigated by a PCA. An Anova was used to identify the significant PCs. These were visualised in plots.
- Evaluation of Sub-hypothesis 3d: Form differences between pre-2000 BP and post-2000 BP female samples were investigated by a PCA. An Anova was used to identify the significant PCs. These were visualised in plots.
- Evaluation of Sub-hypothesis 3e: The allometric shape vector for males was plotted against radiocarbon date to investigate size-related shape (allometry) change during the last 4000 years. To investigate the timing and magnitude of allometric shape changes during the Holocene, the allometric shape vector for the entire male sample (12 000 – 500 BP) was plotted against radiocarbon date. The timing and magnitude of allometric shape changes were also investigated by plotting median and standard deviations of allometric shape vector values against radiocarbon date.
- Evaluation of Sub-hypothesis 3f: The allometric shape vector for females was plotted against radiocarbon date to investigate size-related shape (allometry) change during the last 4000 years.

CHAPTER SEVEN

RESULTS

REPEATABILITY

The repeatability of the 190 individual linear measurements is tested and presented in Appendix 1. The repeatability for all 190 linear measurements is above 97.0% with three exceptions (D-ZYO at 94.2%, ZYO-FMO at 95.4% and BA-TSP at 96.8%). The median repeatability is 99.5%. The median repeatability of the 48 selected linear measurements (in bold) is slightly lower at 99.0%. The repeatability of the 20 landmarks is also evaluated. In all 20 cases, repeatability is greater than 98.0%, with the median repeatability of each landmark at 99.4% (Appendix 2). In the analysis of both the linear measurements and the individual landmarks, repeatability estimates are so high that it is reasonable to conclude that measurement error had little effect on morphological analyses.

THE ANTIQUITY OF KHOESAN CRANIOFACIAL MORPHOLOGY – EVALUATION OF HYPOTHESIS 1:

COMPARISON OF MAHALANOBIS DISTANCES (D) BETWEEN PRE-5000 BP INDIVIDUALS

This section evaluates Sub-hypothesis 1a, which states that there are no statistically significant morphological differences between crania in the pre-5000 BP sample. Table 7.1 presents the inter-individual Mahalanobis distances (D) between crania pre-dating

Specimen	Date (BP)	SAM-AP 6272	UCT180	SAM-AP 4182	SAM-AP 5055	UCT156	SAM-AP 4692
SAM-AP 6272	5830±80	0					
UCT180	6180±70	9.18	0				
SAM-AP 4182	6811±36	9.84	9.18	0			
SAM-AP 5055	6995±50	10.20	9.98	9.28	0		
UCT156	10110±80	9.83	10.47	9.83	10.25	0	
SAM-AP 4692	*ca.* 12000	9.77	10.98	10.00	10.36	9.24	0

Table 7.1: Mahalanobis distances (D) among the six pre-5000 BP crania.

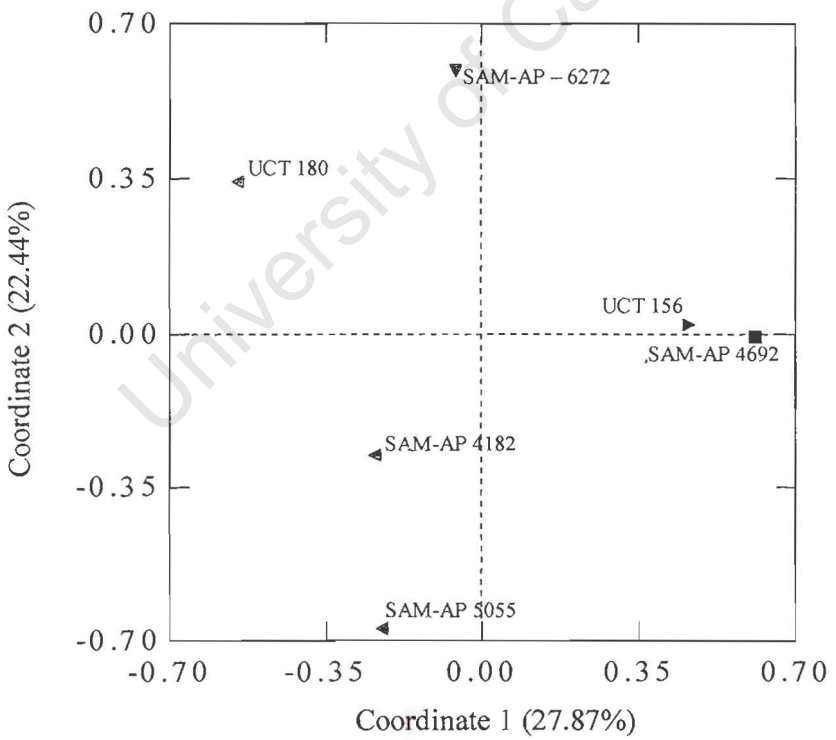

Figure 7.1: Principal coordinates plot of distances among the six pre-5000 BP crania. The first two coordinates are illustrated.

5000 BP. Despite approximately 2000 years of temporal separation, SAM-AP 4692 and UCT 156 (*ca.* 12 000 BP and 10 111 ± 80 BP respectively) are morphologically very similar (D = 9.24). When these two Late Pleistocene/very early Holocene crania are compared to four crania from the early mid-Holocene, namely SAM-AP 6272, UCT 180, SAM-AP 4182 and SAM-AP 5055 (5830 ± 80 BP, 6180 ± 70 BP, 6811 ± 36 BP and 6995 ± 50 BP respectively), inter-individual distances increase slightly, ranging from a low of 9.77 (SAM-AP 4692 vs. SAM-AP 6272) to a high of 10.98 (SAM-AP 4692 vs. UCT 180). Within the entire pre-5000 BP sample, none of the inter-individual distances are significant at the $p \leq 0.05$ level (D=11.40), using the Defrise-Gussenhoven (1967) criteria (Table 7.1). Figure 7.1 presents a principal coordinates plot of the distance values in Table 7.1. This visualisation of the distances confirms that the two Late Pleistocene/very early Holocene crania exhibit greater similarity to each other than they do to the four early mid-Holocene crania. Based on this limited sample size, the Mahalanobis distances indicate that early Holocene Khoesan populations were quite homogenous in terms of cranial morphology.

COMPARISON OF MAHALANOBIS DISTANCES (D) BETWEEN PRE-5000 BP CRANIA AND CRANIA FROM LATER KHOESAN POPULATIONS

This section, and the next, evaluates sub-hypothesis 1b which states that pre-5000 BP crania fall within the range of morphological variation of the 5000 – 2000 BP cranial sample. Appendices 3 and 4 present the Mahalanobis distances between all crania; distances between males are presented in Appendix 3 and distances between females in Appendix 4. Focussing just on the pre-2000 BP sample, the two male Late Pleistocene/

Catalogue no.	Date (BP)	Median	Mean	Std. Deviation
SAM-AP5035b	2011±30	10.45	10.41	0.74
SAM-AP 1443	2050±50	9.91	9.92	0.77
UCT387	2055±40	9.41	9.38	0.75
SAM-AP 1142	2090±27	9.25	9.37	0.75
UCT220	2100±21	9.33	9.30	0.81
SAM-AP 4636	2130±45	9.63	9.50	0.72
SAM-AP 6313b	2140±29	9.28	9.45	0.81
SAM-AP 5082	2150±60	9.36	9.31	0.70
SAM-AP 1441	2170±60	9.52	9.51	0.78
UCT134	2210±40	10.04	10.08	0.72
SAM-AP 4942	2220±45	9.76	9.75	0.90
A1114	2271±33	10.19	10.20	0.77
UCT107	2290±50	9.42	9.42	0.87
SAM-AP 6043	2295±28	10.10	10.04	0.76
SAM-AP 34	2310±25	9.54	9.43	0.86
SAM-AP 1146	2321±28	9.50	9.56	0.78
NMB82	2335±40	9.50	9.43	0.72
SAM-AP 4899	2440±60	8.95	8.98	0.72
ALB222	2540±60	9.68	9.69	0.77
ALB301	2570±50	10.23	10.13	0.76
A1115	2588±28	10.23	10.24	0.77
UCT167	2695±45	8.94	8.90	0.90
UCT445	2720±60	10.44	10.40	0.86
SAM-AP 5049	2740±50	8.97	9.00	0.86
SAM-AP 5048	2780±60	9.75	9.83	0.87
UCT162	2880±50	10.08	10.08	0.77
SAM-AP 6147	2920±60	9.29	9.35	0.91
SAM-AP 6071	2935±32	9.06	9.16	0.81
SAM-AP 6317	2970±60	9.47	9.55	0.74
NMB1242	3030±26	9.21	9.35	0.70
NMB1273	3050±60	9.07	9.09	0.83
NMB1202	3140±50	9.26	9.25	0.82
SAM-AP 1145	3210±70	9.37	9.48	0.78
NMB4	3236±33	10.61	10.44	0.69
SAM-AP 6318	3310±60	9.20	9.15	0.88
SAM-AP 1879	3440±60	8.79	8.86	0.62
SAM-AP 31	3576±30	10.54	10.56	0.75
SAM-AP 4931	3750±60	9.47	9.43	0.91
SAM-AP 32	3754±35	9.62	9.68	0.72
A1124	4320±32	11.13	11.14	0.72
UCT112	4445±50	9.63	9.54	0.82
ALB131	4700±60	9.28	9.15	0.83
NMB1275	4850±60	8.71	8.84	0.73
SAM-AP 6272	5830±80	9.90	9.87	0.70
UCT180	6180±70	9.99	9.94	0.76
SAM-AP 4182	6811±36	10.02	9.92	0.89
SAM-AP 5055	6995±50	9.86	9.91	0.76

Table continued:

UCT156	10110±80	10.25	10.24	0.65
SAM-AP 4692	*ca.* 12000	10.33	10.18	0.85

Table 7.2: Median, mean and standard deviation of Mahalanobis distances (D) for individual male crania in the pre-2000 BP sample relative to all other crania in the sample.

very early Holocene crania, SAM-AP 4692 and UCT 156, are compared to a sample of 47 male crania falling in the 7000 BP to 2000 BP time period. Only four significantly different distances ($p \leq 0.05$) are identified between these two very early crania and individual crania from the 7000 BP to 2000 BP time period. SAM-AP 4692 differs significantly from UCT 445 (2720 ± 60 BP) and A 1124 (4320 ± 32 BP), while UCT 156 differs significantly from NMB 4 (3236 ± 33 BP) and A 1124 (4320 ± 32 BP). In the case of the early mid-Holocene sample (SAM-AP 6272, UCT 180, SAM-AP 4182 and SAM-AP 5055), again only four statistically significant distances are observable between these crania and later crania. SAM-AP 6272 is significantly different from A 1124 (4320 ± 32 BP), UCT 180 is significantly different from SAM-6043 (2295 ± 28 BP), and SAM-AP 5055 is significantly different from A 1114 (2271 ± 33 BP) and SAM-AP 31 (3576 ± 30 BP).

Table 7.2 presents the median, mean and standard deviation of Mahalanobis distances for all male crania in the pre-2000 BP sample, relative to all other crania in the sample. Although the median and mean inter-individual distances displayed by SAM-AP 4692 and UCT 156 are among the largest in the sample, at 10.25 and 10.24, and 10.33 and 10.18, respectively, they are within the range of variation seen in the sample. Five other later crania have larger median and mean distance values (A 1124, SAM-AP 31, NMB 4, UCT 445, SAM-AP 5035b). The four early mid-Holocene crania display slightly lower

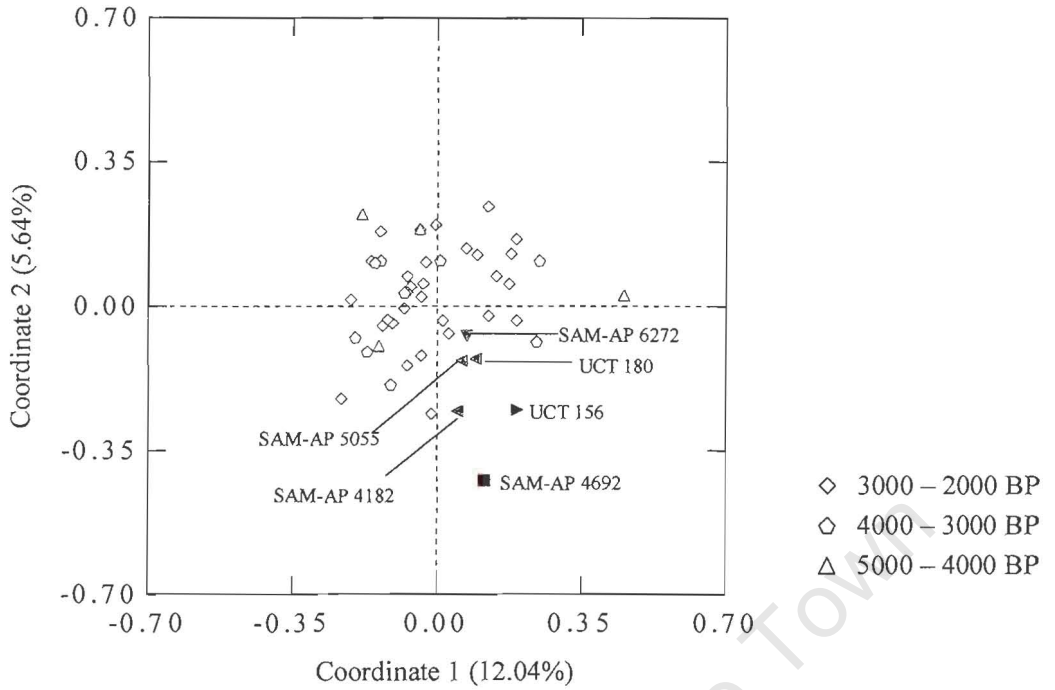

Figure 7.2: Principal coordinates plot of distances among all pre-2000 BP crania.

median and mean inter-individual distances than the two Late Pleistocene/very early Holocene crania. The distance values of these pre-5000 BP crania are low and comparable to those of crania in the 5000 BP – 2000 BP sample. Interestingly, all standard deviations in the pre-2000 BP sample are less than one, suggesting a relatively homogenous population prior to 2000 BP.

To graphically illustrate distances between individual crania in the pre-2000 BP sample, the values in Appendix 3 are subjected to principal coordinates analysis (Figures 7.2). All crania are relatively tightly grouped, again suggesting a high degree of homogeneity in craniofacial form for the pre-2000 BP sample. The two Late Pleistocene/very early Holocene crania, along with the four other pre-5000 BP crania, form a cluster of their own close to the periphery of the main cluster. While the four early mid-Holocene crania

fall within the main cluster, UCT 156 and SAM-AP 4692 are positioned further away. Despite the somewhat peripheral positioning of these two early crania, they cannot be considered morphologically distinct, since some later crania are located just as far away from the main cluster as they are. To sum up, the distances show that the two Late Pleistocene/very early Holocene crania and the four mid-Holocene crania fall within the range of variation of later Khoesan crania. Yet these early crania also share certain aspects of morphological patterning that identify them as a subgroup within the general craniofacial morphology of pre-2000 BP Khoesan populations.

MORPHOLOGY THAT CHARACTERISE VARIATION IN PRE-5000 BP CRANIA VERSUS LATER CRANIA

In order to examine the range of variation seen in this sample, and to further identify both the position of the early crania within this range, as well as the primary morphological traits that are associated with these pre-5000 BP crania, a PCA is performed on all male crania pre-dating 2000 BP (unscaled variables). Because the pre-5000 BP sample numbers only six individuals, an ANOVA could not be performed to determine the PCs which best distinguish between them and the later cranial sample. Table 7.3 presents the first 13 eigenvalues (those greater than 1), which indicate that these components collectively explain over 85% of the total variance. The eigenvectors for the first 13 PCs are presented in Appendix 5. Plots of individual loadings on the first three PCs, which explain 40.44% of the total variation, are illustrated in Figures 7.3 and 7.4. Despite the presence of seven weakly negative variables, PC 1 primarily explains overall size and size-related shape. The most positive values on PC 1 (19.05%) represent crania that

	Eigenvalue	% of Variance	Cumulative %
PC1	9.14	19.05	19.05
PC2	6.18	12.87	31.92
PC3	4.09	8.52	40.44
PC4	3.53	7.36	47.80
PC5	2.97	6.19	53.99
PC6	2.72	5.66	59.64
PC7	2.39	4.99	64.63
PC8	2.22	4.62	69.25
PC9	2.04	4.24	73.49
PC10	1.68	3.50	76.99
PC11	1.57	3.26	80.25
PC12	1.41	2.94	83.19
PC13	1.12	2.32	85.52

Table 7.3: Primary characteristics of the first thirteen principal components of a principal components analysis of pre-2000 BP male crania.

combine large frontal regions with long and broad faces, projecting upper-faces and broad posterior neurocranial regions. The most negative values on PC 1 represent crania that combine small frontal regions with short and narrow faces, retracted upper-faces and narrow posterior neurocranial regions. The most positive values on PC 2 (12.87%) represent crania that exhibit expanded neurocranial dimensions relative to facial dimensions. The most negative values represent crania that exhibit reduced neurocranial dimensions relative to facial dimensions. On PC 3 (8.52%) the most positive values relate to morphologies which display an increase in the superior aspects of the neurocranium relative to its inferior aspects. This neurocranial morphology is combined with reductions in several facial dimensions. The most negative values relate to morphologies which display a decrease in the superior aspects of the neurocranium relative to its inferior aspects. This is associated with increases in some facial dimensions.

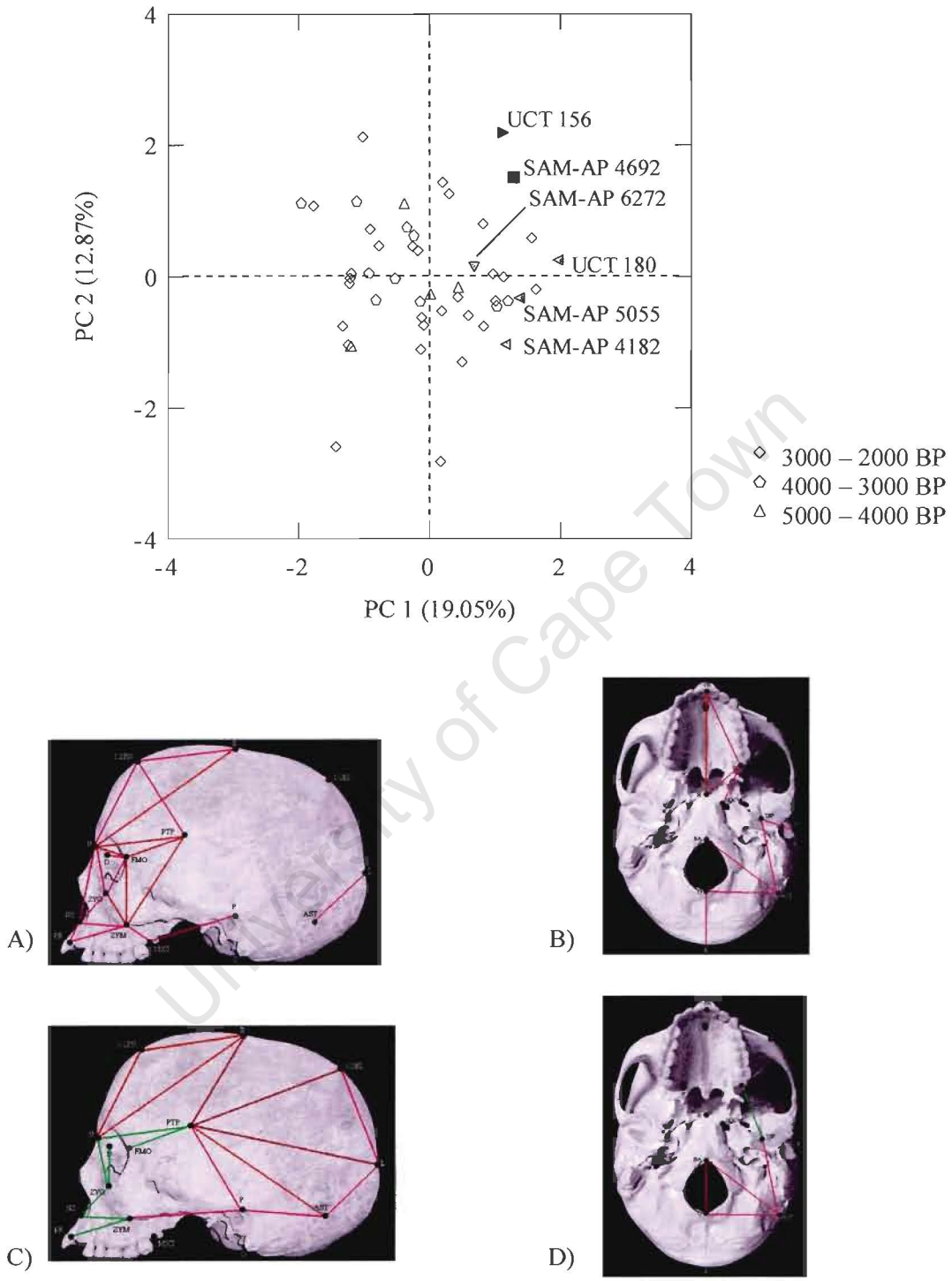

Figure 7.3: Plot of PC 1 and PC 2 of a principal components analysis of pre-2000 BP male crania. Strongly positive and negative loadings on the eigenvectors for PC 1 (A and B) and PC 2 (C and D) are illustrated. Pink represents loadings from 0.1 to 0.19, blood red represents loadings from 0.2 to 0.29 and dark red represents loadings above 0.3. Light green represents loadings from -0.1 to -0.19.

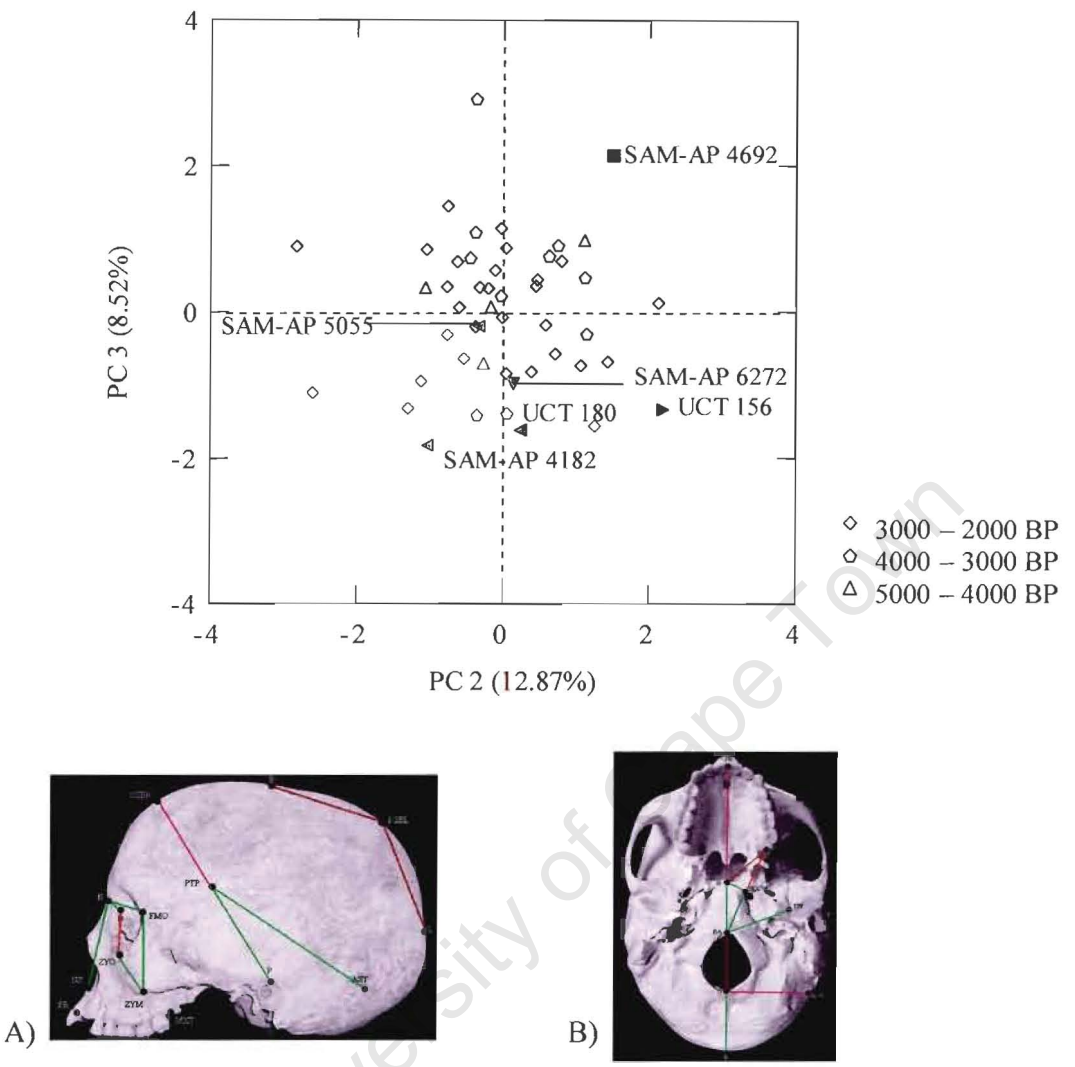

Figure 7.4: Plot of PC 2 and PC 3 of a principal components analysis of pre-2000 BP male crania. Strongly positive and negative loadings on the eigenvectors for PC 3 (A and B) are illustrated. Pink represents loadings from 0.1 to 0.19, blood red represents loadings from 0.2 to 0.29 and dark red represents loadings above 0.3. Light green represents loadings from -0.1 to -0.19.

As illustrated in Figure 7.3 all the pre-5000 BP crania display positive values on PC1. The mid-Holocene cranium UCT 180 has the largest, most projecting face of any pre-2000 BP cranium. As a group, the facial and frontal regions of all pre-5000 BP crania are generally larger, with more projecting upper faces, relative to the majority of later crania. This said, the facial morphology of pre-5000 BP crania still fall within the range of

variation of later populations. This supports previous observations that these early crania resemble later Khoesan populations in terms of facial morphology. On PC 2, SAM-AP 4692 and UCT 156 exhibit neurocrania that rank among the highest, broadest and longest in the sample (Figures 7.3 and 7.4). The early mid-Holocene individuals fall comfortably within the range of variation of later populations in terms of relative neurocranial shape. On PC 3, SAM-AP 4692 and NMB 4 (a cranium dating to 3236 ± 33 BP) are separated from the rest of the pre-2000 BP sample based on prominent frontal and posterior parietal development (Figures 7.4). In sum, the results of the principal components analyses indicate that the terminal Pleistocene/very early Holocene crania, SAM-AP 4692 and UCT 156, and the early mid-Holocene crania, SAM-AP 6272, UCT 180, SAM-AP 4182 and SAM-AP 5055, are characterised by long and broad faces and frontal bones, and pronounced upper-facial projection. SAM-AP 4692 and UCT 156 are also characterised by neurocranial dimensions that are expanded relative to facial dimensions, a trait which distinguish them from most pre-2000 BP crania, including other pre-5000 BP crania. So while the pre-5000 BP crania are often larger than crania in the 5000 to 2000 BP sample, they are still similar in overall morphology.

REDUCTION IN CRANIAL SIZE BETWEEN 4000 BP AND 3000 BP – EVALUATION OF HYPOTHESIS 2:

TEMPORAL ANALYSIS OF CENTROID SIZE OVER THE LAST 12 000 YEARS

This and the following sections evaluate Sub-hypotheses 2a and 2b which hypothesise that male and female cranial size was smallest between 4000 and 3000 BP. Centroid sizes

are calculated for each cranium in the study sample and are presented in Appendix 6 for males and Appendix 7 for females . These values range from a minimum of 292.57 to a

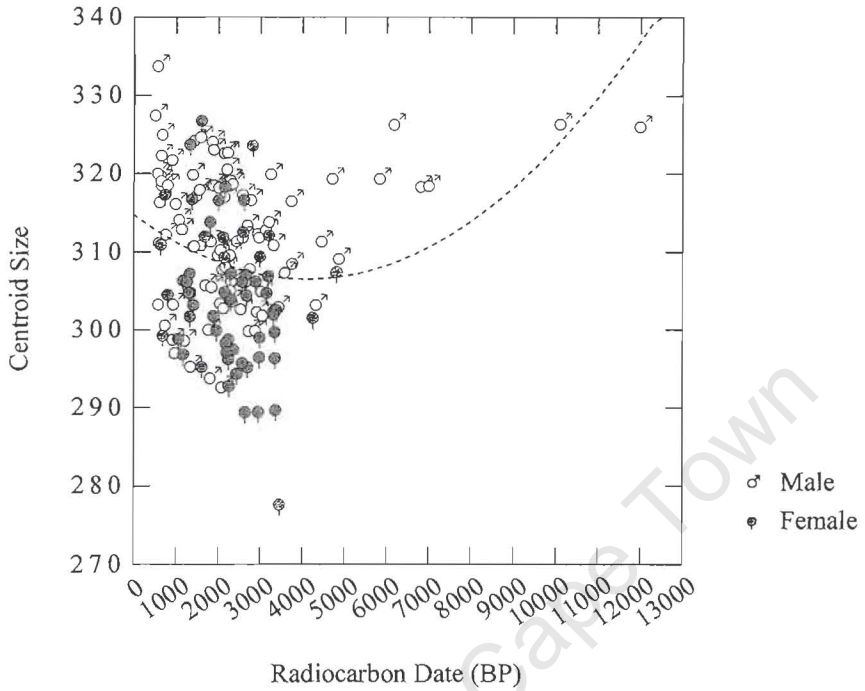

Figure 7.5: Combined plot of individual male and female centroid size values (all crania) against radiocarbon date. Curve represents a quadratic regression model.

maximum of 333.72 for males, and a minimum of 277.56 to a maximum of 326.72 for females. Figure 7.5 presents a combined plot of male and female cranial centroid sizes over the last 12 000 years. Some of the largest crania in the sample pre-date 5000 BP, including three very large crania (SAM-AP 4692, UCT 156 and UCT 180). Whether large cranial size was the norm during this early period cannot be answered conclusively on the basis of the small pre-5000 BP cranial sample included in this study. However, based on previous observations of large terminal Pleistocene/early Holocene cranial size (Rightmire 1974; Braüer and Rösing 1989), and the results of Pfeiffer and Sealy's (2006) study which indicated that stature levels were high during the early Holocene, it is reasonable to conclude that cranial size was probably generally large during the early

Holocene. Nonetheless, the results of this study, as they relate to the early Holocene sample, should be seen as preliminary. More concrete statements can be made about cranial size during the last 5000 years. The large post-5000 BP male and female samples demonstrate considerable diversity in cranial size, although some general patterns do emerge. For instance, the cranial sizes of both sexes show a decrease between 4000 and 2000 BP. A few extremely small female crania are also present at this time. After 2000 BP, several large crania occur, including a few large female crania. A quadratic curve fitted to this plot indicates a general reduction in cranial size coinciding roughly with the end of the mid-Holocene, and a subsequent recovery during the late Holocene. Although weak, this pattern is significant (r^2=0.11, F=8.08, p<0.001).

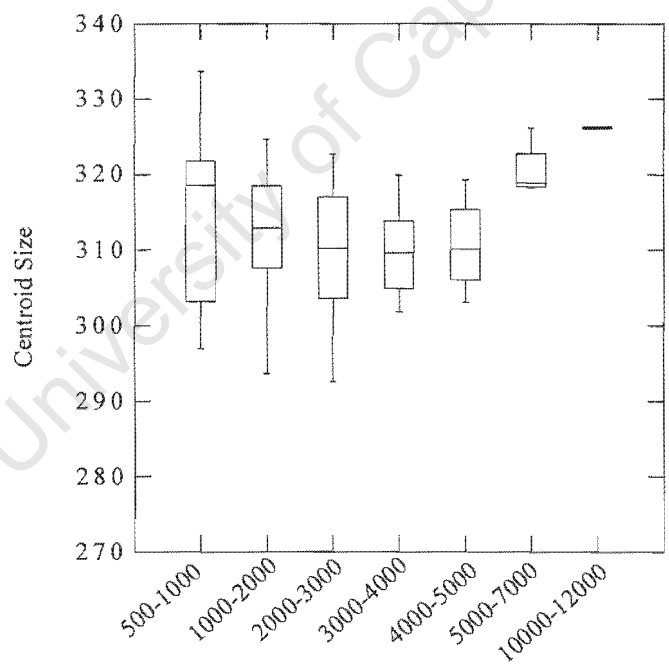

Figure 7.6: Box plots of male centroid size for the last 12 000 years. The vertical line in the centre of the box marks the median of the sample. The length of each box represents the range within which the central 50% of the values fall, with the box edges at the first and third quartiles. The whiskers extend to the highest and lowest values of the interquartile range. Time is divided into two 2000 year intervals for the pre-5000 BP sample, four 1000 year intervals for the 5000 to 1000 BP sample, and a 500 year interval for the post 1000 BP sample.

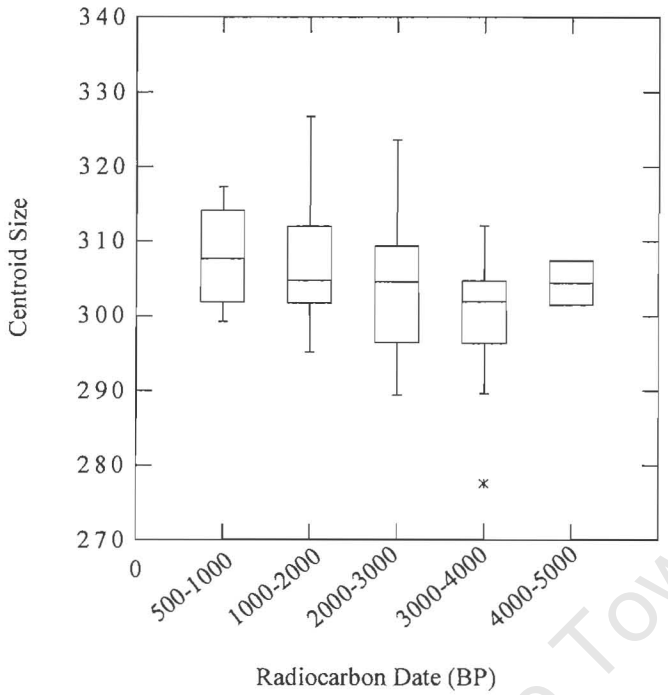

Figure 7.7: Box plots of female centroid size for the last 5000 years. The vertical line in the centre of the box marks the median of the sample. The length of each box represents the range within which the central 50% of the values fall, with the box edges at the first and third quartiles. The whiskers extend to the highest and lowest values of the interquartile range. The asterisk represents a value falling outside of the lowest value of the interquartile range for the 3000 to 4000 BP sample. Time is divided into four 1000 year intervals for 5000 to 1000 BP sample, and a 500 year interval for the post 1000 BP sample.

TIMING OF THE REDUCTION

In Figure 7.6, the timing of the reduction and subsequent increase in cranial size is further explored for the male sample alone. Median male cranial size is low throughout the time period between 5000 and 2000 BP, but it is at its lowest between 4000 and 3000 BP. In the female sample, which only covers the last 5000 years, median cranial size is also at its lowest between 4000 and 3000 BP, after which there is a gradual increase (Figure 7.7). Despite this general increase in cranial size after 3000 BP, large standard deviations in centroid size indicate substantial variation in both male and female cranial size during this period. Again, the apparent reduction in cranial size during the mid-Holocene

(observable in the males) should be viewed as preliminary until a substantially larger pre-5000 BP sample can be included. The next section focuses on the last 4000 years and investigates the significance of the apparent increase in cranial size after the low achieved between 4000 and 3000 BP.

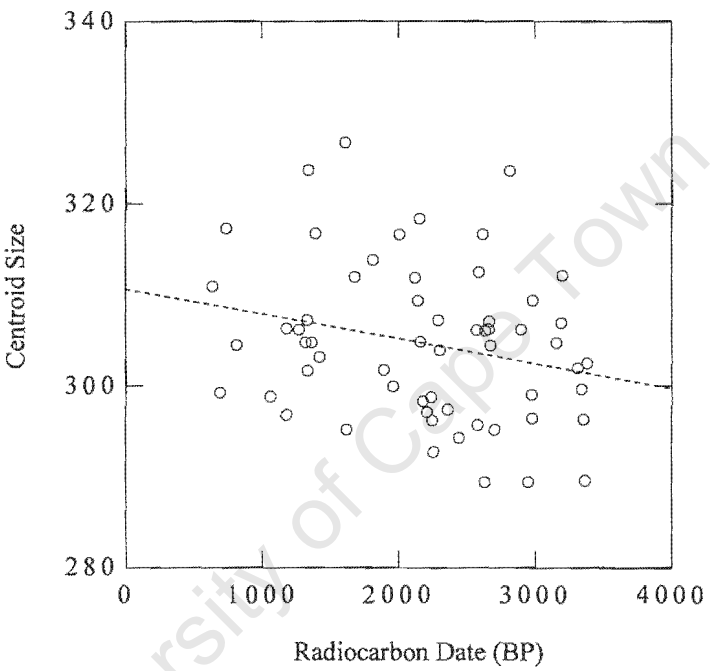

Figure 7.8: Plot of individual female centroid size values for the last 5000 years against radiocarbon date. Curve represents a linear regression model.

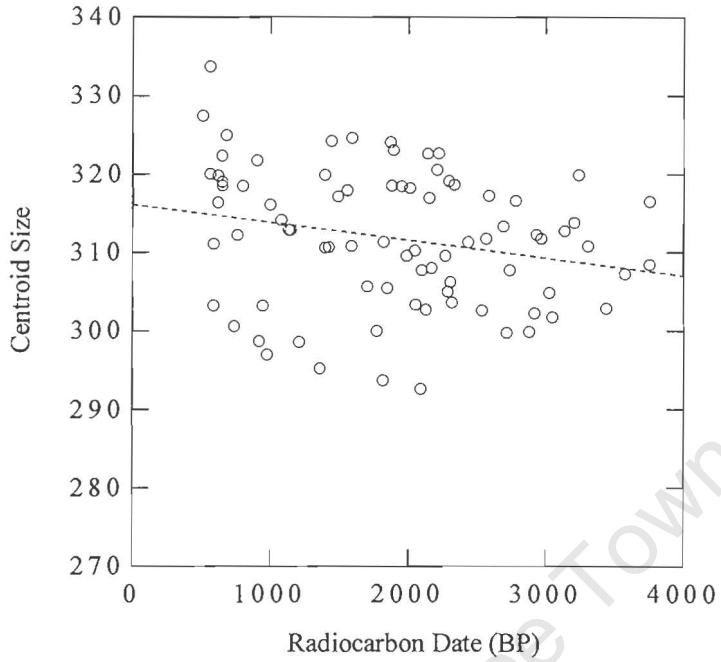

Figure 7.9: Plot of individual male centroid size values for the last 5000 years against radiocarbon date. Curve represents a linear regression model.

TEMPORAL ANALYSIS OF CENTROID SIZE OVER THE LAST 4000 YEARS

Figures 7.8 and 7.9 present plots of female and male centroid size, respectively, over the last 4000 years. In Figure 7.8, the fitted linear curve indicates a relatively weak, yet significant, increase in female cranial size over the last 4000 years (r^2=0.09, F=5.76, p=0.02). Similarly, in the male sample, the fitted linear curve indicates a weak, yet significant increase in cranial size over the last 4000 years (r^2=0.05, F=4.51, p=0.04). These results mirror Pfeiffer and Sealy's (2006) demonstration of a significant increase in stature over the last 3000 years.

THE INTRODUCTION OF HERDING AND THE QUESTION OF BIOLOGICAL CONTINUITY IN LOCAL POPULATIONS – EVALUATION OF HYPOTHESIS 3:

VARIABILITY IN PRE - 2000 AND POST - 2000 BP POPULATIONS

The biological influence of an immigrant human population on indigenous populations may lead not only to a general change in existing patterns of craniofacial morphology, but also to dramatically increased levels of inter-individual variability. The second phenomenon normally results from the presence of morphologically distinct individuals (the new migrants) amongst local populations, or, gene flow between locals and migrants (Relethford 2001a). Levels of inter-individual variability may also be great in a region where biologically distinct populations coexist without any gene flow occurring. In this section, the post-5000 BP cranial samples of both sexes are analysed to determine whether there was an increase in variability during the last 2000 years. It therefore addresses Sub-hypotheses 3a and 3b which hypothesise that inter-individual cranial variation did not increase in males and females respectively after 2000 BP. Pre-5000 BP crania are excluded from the first part of this analysis so that male and female samples may be evaluated across equal time periods.

Mean and standard deviations of inter-individual Mahalanobis distances for male and female pre-2000 BP and post-2000 BP samples are calculated. The mean inter-individual distance value for males increases from 9.55 to 9.87 ($t=6.14$, $p<0.001$). The mean inter-individual distance value for females increases from 9.30 to 9.71 ($t=5.39$, $p<0.001$). In

Catalogue no.	Date (BP)	Median	Mean	Std. Deviation
UCT262	510±40	9.43	9.47	0.89
NMB1207	560±50	9.55	9.52	0.93
UCT583	560±45	9.09	9.08	0.76
UCT157	587±28	9.54	9.53	0.83
SAM-AP 4867	590±45	9.50	9.42	0.77
SAM-AP 6020	620±30	9.06	9.07	0.89
SAM-AP 5035a	620±35	9.87	9.92	0.88
NMB1219	650±60	9.76	9.93	0.77
NMB1338	650±35	9.76	9.65	0.79
UCT114	650±40	9.48	9.55	0.71
UCT83	680±40	10.10	10.12	0.82
SAM-AP 1446	740±30	9.51	9.62	0.83
SAM-AP 5032	765±25	9.80	9.94	0.82
A2226	800±50	10.40	10.44	0.84
A1154	905±25	9.57	9.61	0.75
UCT70	920±40	9.17	9.19	0.79
UCT60	950±50	9.08	9.09	0.86
SAM-AP 6332	980±50	9.37	9.37	0.79
UCT227	1000±50	8.90	9.02	0.85
SAM-AP 4898	1084±26	9.42	9.41	0.83
SAM-AP 1260	1137±27	10.83	10.88	0.70
A2227	1150±50	11.65	11.70	0.81
SAM-AP 4905	1210±50	9.61	9.62	0.81
SAM-AP 6074	1360±40	9.58	9.61	0.75
NMB1707	1394±24	10.26	10.20	0.75
SAM-AP 6334	1400±50	10.05	9.96	0.81
SAM-AP 4874	1426±29	8.60	8.66	0.91
SAM-AP 6149	1440±70	10.03	10.04	0.80
SAM-AP 5083	1490±50	9.17	9.17	0.71
SAM-AP 6213	1558±27	10.15	10.13	0.75
UCT109	1590±50	9.71	9.68	0.84
NMB83	1590±40	10.34	10.29	0.73
SAM-AP 320g	1707±27	10.09	10.13	0.78
SAM-AP 4630	1775±80	10.75	10.82	0.78
A1166	1818±27	10.51	10.51	0.98
SAM-AP 6041a	1824±27	9.91	9.82	0.79
A1152	1850±35	10.61	10.58	0.82
UCT429	1870±35	10.39	10.35	0.80
SAM-AP 1473	1880±60	9.47	9.52	0.84
SAM-AP 4901	1892±28	9.91	9.91	0.83
SAM-AP 6264	1950±60	8.82	8.85	0.89
SAM-AP 3053	1990±50	9.81	9.88	0.91
SAM-AP 5035b	2011±30	10.36	10.39	0.84
SAM-AP 1443	2050±50	9.98	9.92	0.84
UCT387	2055±40	9.46	9.51	0.85
SAM-AP 1142	2090±27	9.35	9.40	0.68
UCT220	2100±21	9.58	9.54	0.78
SAM-AP 4636	2130±45	9.45	9.49	0.75
SAM-AP 6313b	2140±29	9.26	9.44	0.84

Table continued:

SAM-AP 5082	2150±60	9.35	9.39	0.94
SAM-AP 1441	2170±60	9.52	9.50	0.77
UCT134	2210±40	10.14	10.21	0.83
SAM-AP 4942	2220±45	9.73	9.78	0.92
A1114	2271±33	10.29	10.25	0.68
UCT107	2290±50	9.43	9.47	0.90
SAM-AP 6043	2295±28	10.07	10.01	0.81
SAM-AP 34	2310±25	9.63	9.46	0.90
SAM-AP 1146	2321±28	9.52	9.56	0.84
NMB82	2335±40	9.49	9.42	0.74
SAM-AP 4899	2440±60	8.99	9.05	0.78
ALB222	2540±60	9.66	9.70	0.75
ALB301	2570±50	10.03	10.08	0.81
A1115	2588±28	10.20	10.24	0.75
UCT167	2695±45	8.96	8.97	0.96
UCT445	2720±60	10.34	10.37	0.80
SAM-AP 5049	2740±50	8.97	9.06	0.89
SAM-AP 5048	2780±60	9.82	9.90	0.86
UCT162	2880±50	9.96	9.96	0.77
SAM-AP 6147	2920±60	9.42	9.44	0.94
SAM-AP 6071	2935±32	9.19	9.25	0.82
SAM-AP 6317	2970±60	9.63	9.63	0.75
NMB1242	3030±26	9.36	9.46	0.78
NMB1273	3050±60	9.14	9.16	0.89
NMB1202	3140±50	9.26	9.31	0.87
SAM-AP 1145	3210±70	9.37	9.45	0.77
NMB4	3236±33	10.57	10.49	0.83
SAM-AP 6318	3310±60	9.28	9.21	0.86
SAM-AP 1879	3440±60	8.93	8.93	0.77
SAM-AP 31	3576±30	10.49	10.57	0.81
SAM-AP 4931	3750±60	9.47	9.52	0.86
SAM-AP 32	3754±35	9.55	9.66	0.84
A1124	4320±32	11.03	11.02	0.75
UCT112	4445±50	9.68	9.61	0.83
ALB131	4700±60	9.22	9.24	0.94
NMB1275	4850±60	8.71	8.84	0.83

Table 7.4: Median, mean and standard deviations of Mahalanobis distances (D) between individual male crania and all other male crania in the post-5000 BP sample.

Catalogue no.	Date (BP)	Median	Mean	Std. Deviation
A1153	636±26	9.6	9.7	0.8
SAM-AP 4180	688±27	10.5	10.5	0.8
UCT582	740± 40	9.0	9.1	0.9
SAM-AP 5012	812±26	8.8	8.8	0.9
A1117	1060±50	9.1	9.3	0.9
SAM-AP 1247	1180±50	10.1	10.2	0.8
ALB244(1)	1180±50	9.5	9.7	0.9
UCT94	1270±40	8.8	8.9	0.9
SAM-AP 4314	1319±25	9.2	9.2	0.9
SAM-AP 6075	1330±40	9.2	9.1	0.9
SAM-AP 4669	1333±25	10.8	10.8	0.6
UCT75	1340±40	9.8	9.9	0.8
SAM-AP 4920a	1364±32	9.9	10.0	0.8
SAM-AP 5034	1390±40	9.4	9.2	0.8
NMB5	1423±26	9.1	9.1	0.9
SAM-AP 4790	1610±150	10.2	10.2	0.8
ALB323	1620±35	9.8	9.8	0.8
UCT55	1680±40	9.7	9.8	0.9
SAM-AP 4659	1815±29	9.3	9.4	0.8
A1127	1891±29	9.5	9.8	0.8
UCT120	1960±50	9.1	9.0	0.9
SAM-AP 5041	2010±50	9.1	9.1	0.8
SAM-AP 6260a	2120±60	9.5	9.6	0.9
UCT78	2145±40	8.1	8.2	0.8
SAM-AP 278g	2158±28	8.8	9.0	1.0
SAM-AP 6313a	2161±30	9.2	9.1	0.9
NMB1203	2180±50	9.7	9.6	0.8
NMB1204	2210±35	9.1	8.9	0.9
UCT436	2240±60	9.6	9.6	0.8
SAM-AP 4301	2250±30	8.7	8.8	1.0
SAM-AP 4312	2260±170	9.8	9.8	0.8
SAM-AP 4299	2294±29	9.3	9.3	0.9
SAM-AP 4300	2304±29	9.3	9.2	0.8
UCT164	2360±30	10.0	10.0	0.8
SAM-AP 39	2448±29	9.1	9.1	0.9
SAM-AP 5070	2573±31	10.3	10.4	0.8
SAM-AP 5050	2580±60	9.4	9.4	0.8
NMB1639	2590±60	10.7	10.6	0.8
SAM-AP 1878	2620±35	11.0	11.0	0.8
SAM-AP 5069	2634±28	9.9	10.0	0.8
SAM-AP 4906a	2635±29	8.2	8.2	0.9
SAM-AP 5095	2660±70	9.6	9.6	0.8
SAM-AP 4627	2665±27	8.8	9.0	1.0
SAM-AP 4202	2673±29	8.6	8.8	0.9
NMB86	2705±40	9.1	9.2	0.9
NMB1827	2815±40	9.3	9.3	0.9
UCT421	2895±45	9.7	9.8	0.8
A1172	2950±40	10.2	10.2	0.7
SAM-AP 4906b	2977±33	9.0	9.0	0.9

Table continued:

UCT435	2980±60	9.4	9.4	0.8
UCT343	2985±45	9.0	9.0	0.8
SAM-AP 1128	3156±33	9.4	9.3	0.9
SAM-AP 6051	3190±50	9.1	9.1	0.9
SAM-AP 6319	3200±35	10.0	10.0	0.9
SAM-AP 1871	3310±60	8.7	8.7	0.8
ALB354	3340±60	9.0	9.0	0.8
A1112	3355±45	8.8	8.9	0.9
SAM-AP 4974	3363±34	9.5	9.5	0.8
SAM-AP 4298	3380±33	8.3	8.4	0.8
UCT161	3451±26	9.2	9.4	0.9
NMB1640	4240±70	10.3	10.3	0.8
A1139	4800±50	9.7	9.8	0.7

Table 7.5: Median, mean and standard deviations of Mahalanobis distances (D) between individual female crania and all other female crania in the post-5000 BP sample.

both cases there is a minor, yet significant increase in mean inter-individual distance values. The standard deviation of inter-individual distances increases from 0.934 to 1.05 for males, while it decreases from 1.054 to 0.949 for females. Males therefore display an increase in the levels of inter-individual variation, while females display a decrease. It should be remembered though that the standard deviation is sample specific and may change with the addition or removal of crania.

Median, mean and standard deviations of Mahalanobis distances are also calculated for individual crania, relative to all other crania, to determine whether there are any crania in the post-2000 BP period that displayed divergent morphology, thus accounting for the increase in post-2000 BP mean distances (Tables 7.4 and 7.5). In the male sample, only one cranium in the post-2000 BP sample (A 2227) displays relatively high median and mean distance values. Its standard deviation is, however, similar to those of other crania in the sample, indicating that it varies in a similar manner to these other crania. It is also

noteworthy that A 1124, a cranium dating to 4320 ± 32 BP, displays the second highest median and mean distance values in the sample. In the female sample, the cranium with the highest median and mean distance values is dated to 2620 ± 35 BP (SAM-AP 1878). Thus, although there is an increase in the group means of male and female post-2000 BP samples, this is not due to the inclusion of morphologically divergent crania. This result suggests that large-scale gene flow into the study region probably does not account for the increase in inter-individual morphological distances after 2000 BP. Instead, the increase in post-2000 BP inter-individual distances appears to be population-wide. This suggests that, *in situ* factors, be they genetic or environmental, may be more likely causes. Principal coordinate plots of inter-individual distances for male and female crania over the last 5000 years show substantial overlap between pre-2000 and post-2000 BP samples, suggesting that the two samples are morphologically very similar (Figures 7.10 and 7.11). Again, these results are not consistent with large-scale gene flow into the region.

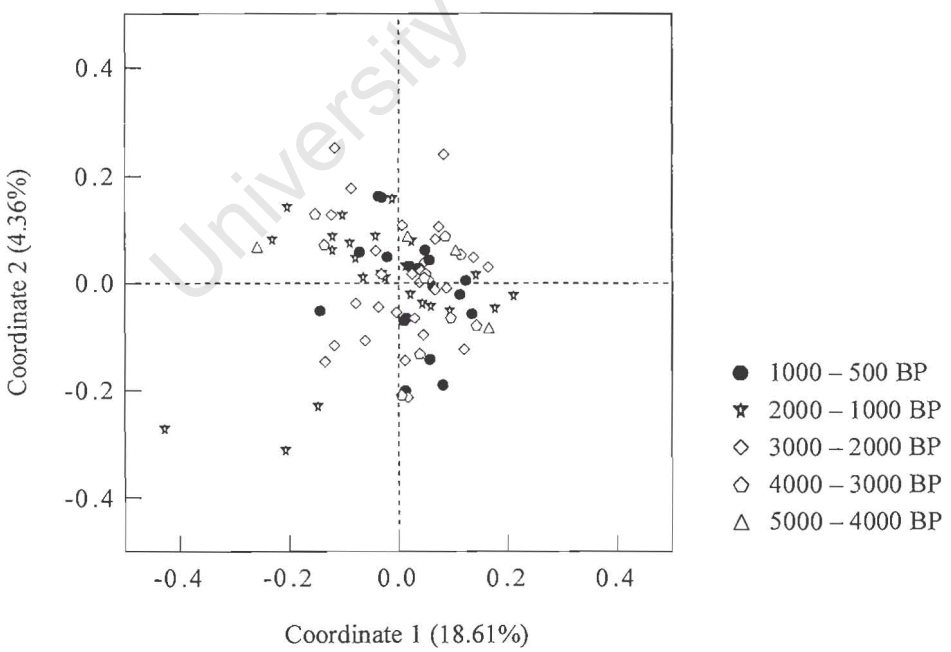

Figure 7.10: Principal coordinates plot of distances among post-5000 BP male crania. The first two coordinates are illustrated.

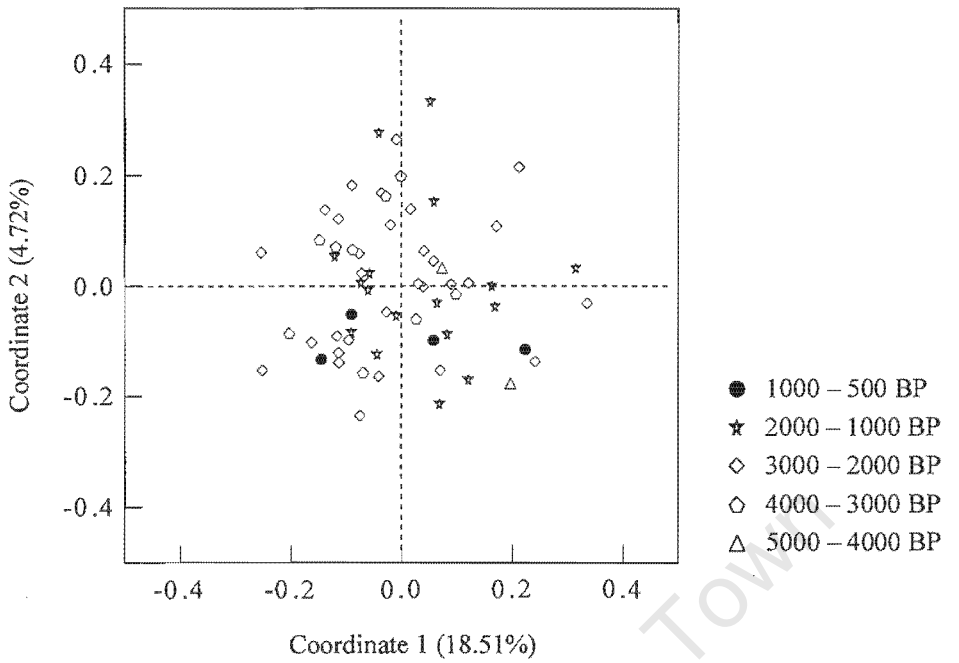

Figure 7.11: Principal coordinates plot of distances among post-5000 BP female crania. The first two coordinates are illustrated.

COMPARISON OF PRE-2000 AND POST-2000 BP CRANIOFACIAL MORPHOLOGY

This section, and the next, set out to answer Sub-hypotheses 3c and 3d, namely that there were no changes in male and female cranial form, respectively, at 2000 BP. PCA is employed to investigate whether there are differences in craniofacial morphology between pre-2000 and post-2000 BP samples. For the male sample, Table 7.6 presents the results of an ANOVA performed on the PCs with eigenvalues greater than one. The variance explained by the first fourteen PCs is presented in Table 7.7. The eigenvectors of these fourteen PCs are presented in Appendix 8. The results of the ANOVA indicate that PCs 1, 2 and 9 were significant ($p \leq 0.05$). These three PCs are plotted and visualised

	df	F	Significance (P=0.05)
PC1	1	**11.01**	0.00
PC2	1	**5.41**	0.02
PC3	1	1.96	0.16
PC4	1	3.05	0.08
PC5	1	0.24	0.63
PC6	1	1.73	0.19
PC7	1	1.04	0.31
PC8	1	0.51	0.48
PC9	1	**4.07**	0.05
PC10	1	1.13	0.29
PC11	1	0.18	0.67
PC12	1	0.07	0.80
PC13	1	0.37	0.55
PC14	1	0.00	0.95

Table 7.6: Results of an analysis of variance (ANOVA) performed on the first fourteen PCs of a PCA of post-5000 BP male crania.

	Eigenvalue	% of Variance	Cumultive %
PC1	10.18	21.21	21.21
PC2	5.28	10.99	32.20
PC3	3.93	8.19	40.40
PC4	3.02	6.29	46.68
PC5	2.77	5.77	52.46
PC6	2.46	5.12	57.57
PC7	2.43	5.07	62.64
PC8	1.90	3.97	66.60
PC9	1.76	3.67	70.27
PC10	1.54	3.20	73.47
PC11	1.41	2.94	76.41
PC12	1.33	2.78	79.19
PC13	1.27	2.64	81.82
PC14	1.14	2.37	84.19

Table 7.7: Primary characteristics of the first fourteen PCs of a PCA of post-5000 BP male crania.

in Figures 7.12 to 7.13. In all plots, 95% confidence intervals are constructed around pre-2000 and post-2000 BP samples. PC 1 (21.21%) primarily represents size and size-related shape. The most positive values along PC 1 represent crania characterised by long and broad faces, pronounced upper-facial regions and long and broad frontal bones. The most

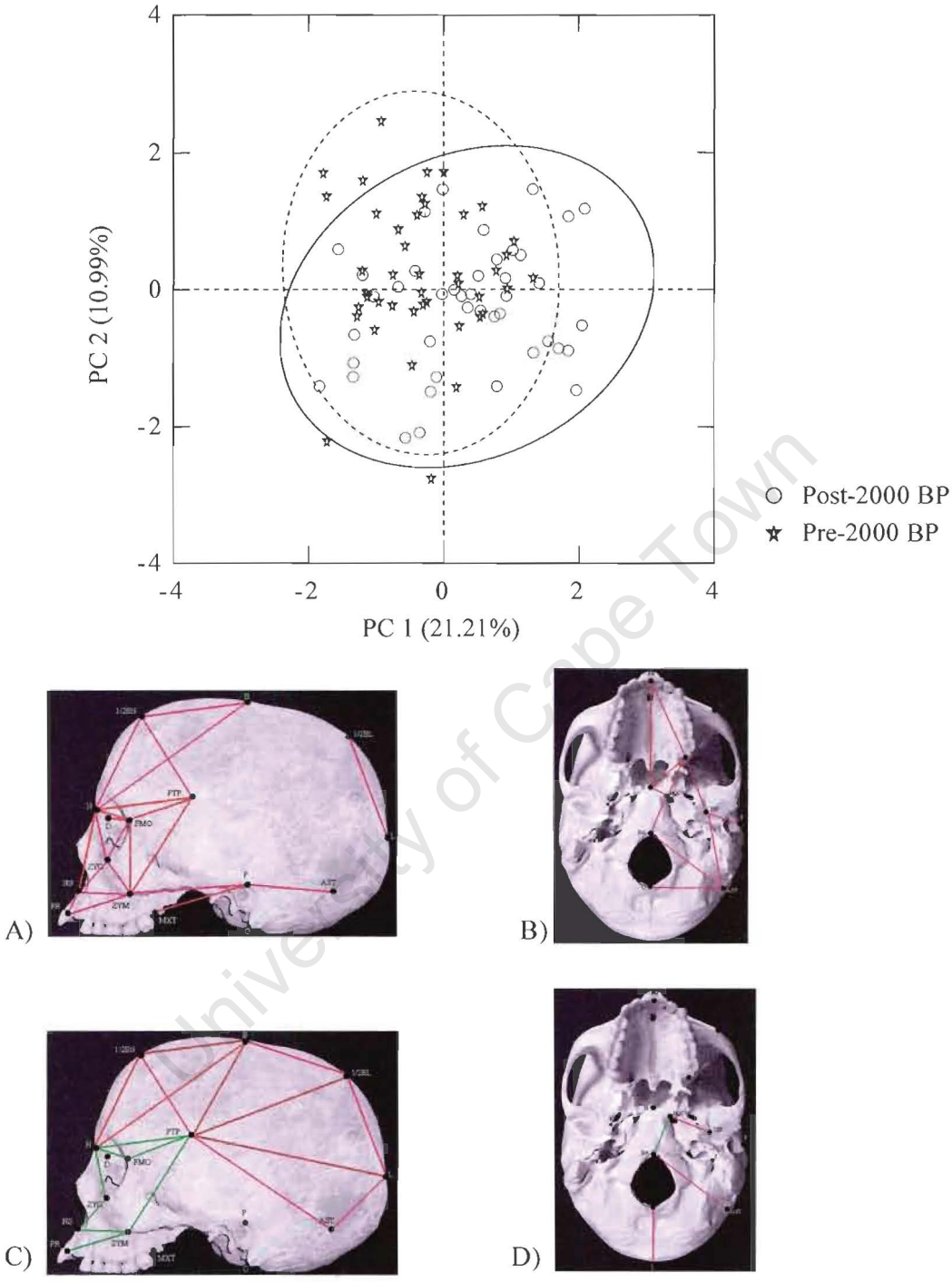

Figure 7.12: Plot of PC 1 and PC 2 of a principal components analysis of post-5000 BP male crania. Strongly positive and negative loadings on the eigenvectors for PC 1 (A and B) and PC 2 (C and D) are illustrated. Pink represents loadings from 0.1 to 0.19, blood red represents loadings from 0.2 to 0.29 and dark red represents loadings above 0.3. Light green represents loadings from -0.1 to -0.19.

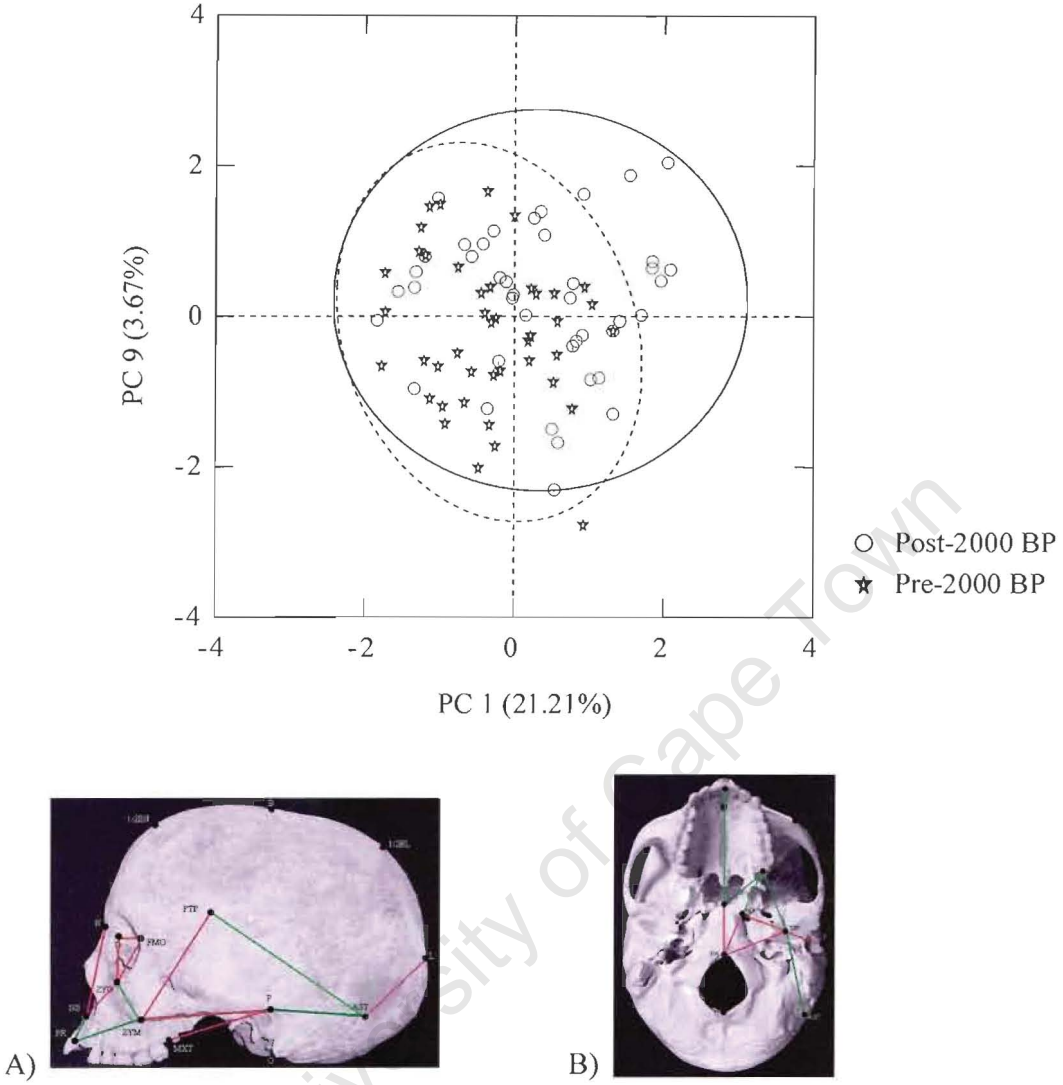

Figure 7.13: Plot of PC 1 and PC 9 of a principal components analysis of post-5000 BP male crania. Strongly positive and negative loadings on the eigenvectors for PC 9 (A and B) are illustrated. Pink represents loadings from 0.1 to 0.19, blood red represents loadings from 0.2 to 0.29 and dark red represents loadings above 0.3. Light green represents loadings from -0.1 to -0.19, lime green represents loadings from -0.2 to -0.29 and dark green represents loadings below -0.3.

negative values along this PC represent crania characterised by small and narrow faces, retracted upper-facial regions, and short and narrow frontal bones. The most positive values on PC 2 (10.99%) represent crania which exhibit expanded neurocranial

dimensions relative to facial dimensions. In turn, the most negative values on this PC represent crania which exhibit reductions in most neurocranial dimensions relative to facial dimensions. The most positive values on PC 9 (3.67%) represent crania characterised by reduced maxillary regions, long and broad upper faces and relatively short, broad posterior neurocranial regions. The most negative values on this PC represent crania characterised by prominent maxillary regions, short and narrow upper-faces, and relatively elongated, narrow posterior neurocranial regions. Despite the ANOVA indicating significant differences between pre-2000 BP and post-2000 BP samples along these three PCs, there is considerable overlap of the samples. However, some trends are observable. Although there is a lot of overlap between these groups along PC 1, some crania from the post-2000 BP period are larger than all crania from the pre-2000 BP period. These crania also have relatively longer and wider faces, prominent upper facial regions, and longer and wider frontal bones. Along PC 2, more pre-2000 BP crania are characterised by expanded neurocranial dimensions relative to facial dimensions. Post-2000 BP crania display the opposite on average, namely reductions in neurocranial dimensions relative to facial dimensions. Along PC 9, more post-2000 BP crania display retracted maxillary regions, elongated upper to mid-facial regions and relatively broad posterior neurocranial regions. In the case of the pre-2000 BP cranial sample, many crania display prominent maxillary regions, reduced upper to mid-facial regions and relatively narrow posterior neurocranial regions.

investigation of the physical remains of humans, particularly cranial remains, has provided valuable, sometimes unexpected information about population continuity or discontinuity. This chapter discusses the implications of the results of the craniometric analyses presented in Chapter 7. As there has been a dearth of recent physical anthropological research into the question of population continuity in the South African LSA, this represents the first effort to reconcile current archaeological information with new biological information.

HOLOCENE VARIATION IN THE KHOESAN CRANIOFACIAL SKELETON

Recent Khoesan populations are typically separated into the San and Khoekhoe. The biological basis of this separation has been researched and debated for well over a century. While recent San groups have generally been regarded as the descendents of pre-2000 BP hunter-gatherers (Laing 1924; Galloway 1937b; Howells 1973; Hausman 1980), the origins of the Khoekhoe have elicited more debate. Typical Khoekhoe cranial morphology has long been purported to have emerged after the introduction of herding, be it through gene flow from incoming herders (Dreyer and Meiring 1937, 1952) or *in situ* differentiation in indigenous populations (Hausman 1980).

Although early researchers have argued that the San and the Khoekhoe differed significantly in overall craniofacial form (Shrubsall 1898, 1907, 1911, 1922), more recent research determined that cranial size is the only reliable trait that could be used to distinguish between members of the two populations. For instance, it is claimed that Khoekhoe crania are large and robust, while those of the San are small and gracile (Stern

CHAPTER EIGHT

DISCUSSION AND CONCLUSION

INTRODUCTION

The question of population continuity during the South African LSA has been the focus of anthropological research for well over a century. It has been investigated from both cultural as well as biological perspectives. Early archaeological studies invariably interpreted cultural change in terms of migrations (e.g. Goodwin and Van Riet Lowe 1929). Similarly, physical anthropologists during the first half of the twentieth century also interpreted variation in craniofacial form through time as evidence of population migrations (Meiring 1937; Louw 1960). Advances in archaeological research over the last 30 years have led to a better understanding of the South African LSA record. Archaeologists were able to demonstrate that temporally related shifts occurred in artefact frequencies and styles, as well as in the composition of food remains. On the basis of these shifts, a modern interpretive framework for the South African LSA was developed which identifies three widely recognisable cultural phases: the Robberg, Oakhurst and Wilton. In contrast to early archaeological studies, recent studies generally attribute changes in the South African LSA to *in situ* development, rather than to the migration of genetically and culturally distinct peoples. The only possible exception however, may relate to the introduction of domestic stock herding at *ca.* 2000 years ago. Although the archaeological evidence is suggestive of long term population continuity during the South African LSA, it is not conclusive. In many regions of the world,

terms of shape, many post-2000 BP crania have long and broad faces, projecting upper faces and long and broad frontal bones, while many pre-2000 BP crania have short and narrow faces, retracted upper-facial regions and short and narrow frontal bones. In addition, while the frontal bones of many post-2000 BP crania recede, those of many pre-2000 BP crania are steep. Analyses indicate that these particular differences in cranial shape may be attributed to allometry. The morphology displayed by many post-2000 BP crania is linked to an increase in cranial size which commenced at approximately 3000 BP, and is not unique to the post-2000 BP period. Pre-5000 BP crania resemble many post-2000 BP crania in terms of size and facial and frontal bone morphology. In addition to allometric changes, many post-2000 BP crania are also characterised by a decrease in neurocranial dimensions relative to facial dimensions. These changes appear to be unrelated to changes in overall cranial size. Again, analyses indicate that this reduction did not commence at 2000 BP but was the culmination of a process that may be traced back to at least the early Holocene. These results suggest that there had *not* been a dramatic change in the craniofacial morphology of indigenous peoples at 2000 BP. Rather, differences between pre- and post-2000 crania are subtle, with much of the variation across the samples originating prior to 2000 BP. The morphological evidence thus points towards biological continuity at 2000 BP. The increase in mean post-2000 BP inter-individual distances is thus unlikely to have been caused by gene flow into the region. *In situ* factors, either genetic or environmental or a combination of both, are more likely explanations for this population-wide increase in variability. The implications of these results will be discussed in the next chapter.

set up to test whether there was biological continuity or discontinuity in the study region at 2000 BP.

Mean inter-individual Mahalanobis distance values indicate a small, yet significant increase in male and female mean inter-individual distances after 2000 BP. At the same time there is an increase in the standard deviation value for the male sample, indicating an increase in variation. In the case of the female sample though, there is a reduction in the standard deviation value. To determine whether any crania in the post-2000 BP period display divergent morphology, thus accounting for the increase in post-2000 BP mean distances, median, mean and standard deviation inter-individual distance values are calculated for each cranium, relative to all other crania, within the last 5000 years. In the male sample, only one cranium in the post-2000 BP sample displays relatively high median and mean distance values. However, its standard deviation is similar to those of other crania in the post-5000 BP sample. These results indicate that the increase in group means after 2000 BP is not caused by the inclusion of morphologically divergent crania. Although there is a slight increase in inter-individual distances in the post-2000 BP sample, principal coordinate plots generated from inter-individual distances fail to identify any substantial differences between pre-2000 and post-2000 BP crania. Despite the slight increase in inter-individual distances in the post-2000 BP sample, these results are not consistent with the migration of genetically distinct herders into the region.

PCA indicate that there are broad form differences between pre-2000 and post-2000 BP samples. Generally, many post-2000 BP crania are larger than pre-2000 BP crania. In

ca. 3000 BP. Hypothesis 2 was set up to test whether cranial size mirrored this mid-Holocene fluctuation in post-cranial dimensions.

Because of the small pre-5000 BP sample, one has to be cautious about interpreting the results from this section. This said, it is significant that the results are consistent with the pattern of fluctuation in post-cranial size identified by Pfeiffer and Sealy (2006). In this analysis, male and female cranial centroid sizes are initially combined and plotted against radiocarbon dates. This plot shows that cranial size is *smallest* for both sexes between 4000 and 3000 BP, although the smallest crania belonged to females. In the case of the males, where the sample extends over a larger part of the Holocene, cranial size is relatively large during the early part of the Holocene, after which it declines. Both males and females display a gradual increase in median cranial size over the last 3000 years. This increase, although relatively weak in the cases of both sexes, is significant. These results thus support Hypothesis 2, namely, that cranial size was smallest between 4000 and 3000 BP.

By *ca.* 2000 BP, people along the Cape Coast started herding domestic stock. Past research (archaeological and biological) has been unable to determine whether domesticates, along with the herding lifestyle, was introduced to the coastal regions by biologically distinct herders from the north, or whether herding entered the region via the acculturation of local hunter-gatherers. If a biologically distinct herder population entered the region, one would expect not only a dramatic increase in craniofacial variation, but also marked changes in overall craniofacial morphology after 2000 BP. Hypothesis 3 was

Holocene crania were also identified and included in the analyses. The results of the current study concur to a large degree with those of previous studies on terminal Pleistocene/early Holocene South African human crania (Howells 1969; Rightmire 1974; Bräuer and Rösing 1989). SAM-AP 4692 and UCT 156, both from the Late Pleistocene/very early Holocene boundary, *resemble* later Khoesan populations in terms of overall morphology, although, they have markedly *larger neurocrania* than most crania in the pre-2000 BP sample. In terms of facial and frontal morphology, all pre-5000 BP crania fall on the edge of the range of variation of crania in the 5000 to 2000 BP sample, suggesting that while they resemble 5000 to 2000 BP crania in overall morphology, pre-5000 BP crania are on average larger and more robust. Although these results support Hypothesis 1, a measure of caution is required. Six crania clearly do not constitute a large enough sample to make firm statements about the craniofacial morphology of populations during the terminal Pleistocene and first half of the Holocene. Therefore, the results of the evaluation of this hypothesis should be seen as preliminary. If in future a large enough sample of complete crania from this early period is assembled, this analysis could be repeated, and the results of this thesis tested. Nonetheless, the results of this analysis are interesting in the context of previous research.

Pfeiffer and Sealy (2006) demonstrated that between 4000 BP and 2000 BP, populations from the southern and south-western regions displayed increasing diversity in stature levels. Between 4000 and 3000 BP, there was a significant reduction in stature from pre-4000 BP levels. Stature levels gradually began to recover to pre-4000 BP levels only after

shape, these crania are characterised by long and broad faces, prominent upper facial regions and long and broad frontal bones. Along PC 2, most pre-2000 BP crania, including four pre-5000 BP crania (SAM-AP 4692, UCT 156, UCT 180 and SAM-AP 6272), exhibit negative values, thus indicating a morphology characterised by neurocranial dimensions that are expanded relative to facial dimensions. On the other hand, most post-2000 BP crania exhibit positive values, thus indicating a morphology characterised by neurocranial dimensions that are reduced relative to facial dimension. In Figure 7.20, PC 2 is plotted against radiocarbon date. From this plot it is evident that there is a minor decrease in male neurocranial dimensions relative to facial dimensions during the course of the Holocene (r^2=0.091, F=4.40, p=0.02). In Figure 7.21, PC 2 for the female sample (5000 – 500 BP) is plotted against radiocarbon date. As in the case of the male sample, there is a minor decrease in relative female neurocranial dimensions during the course of the Holocene (r^2=0.069, F=4.42, p=0.04). Like size and size-related shape change, the reduction in neurocranial dimensions that characterise many post-2000 BP crania had its origin prior to 2000 BP.

SUMMARY OF RESULTS

Hypothesis 1 was set up to investigate the antiquity of Khoesan craniofacial morphology. Only two complete crania from the Late Pleistocene/very early Holocene period, SAM-AP 4692 and UCT 156, were identified and used in this analysis. A third, largely complete cranium, ALB 119 (8260 ± 720 BP GaK-1541) had been identified in previous studies (Bräuer and Rösing 1989). Unfortunately this cranium had to be excluded from this study because it belongs to a sub-adult (A. G. Morris 1992d). Four early mid-

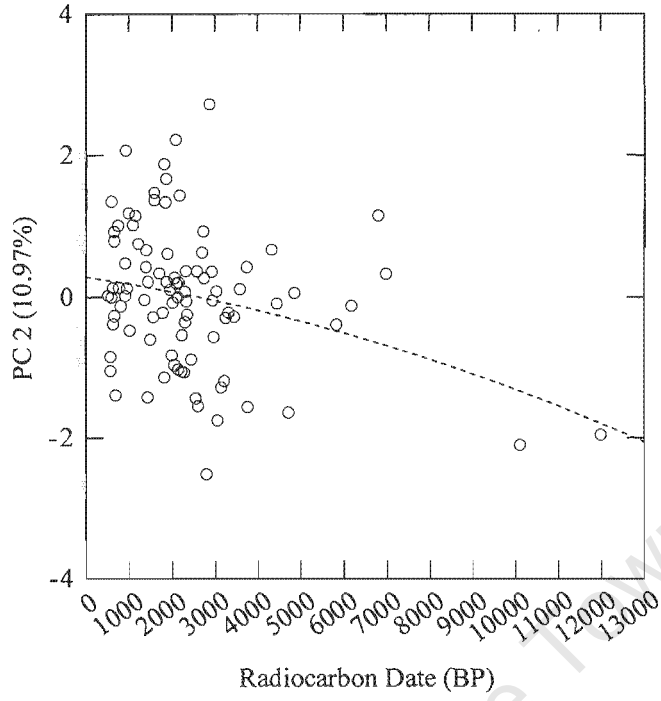

Figure 7.20: Plot of PC 2 of a PCA of all male crania (12 000 to 500 BP) against radiocarbon date. Curve represents a quadratic regression model.

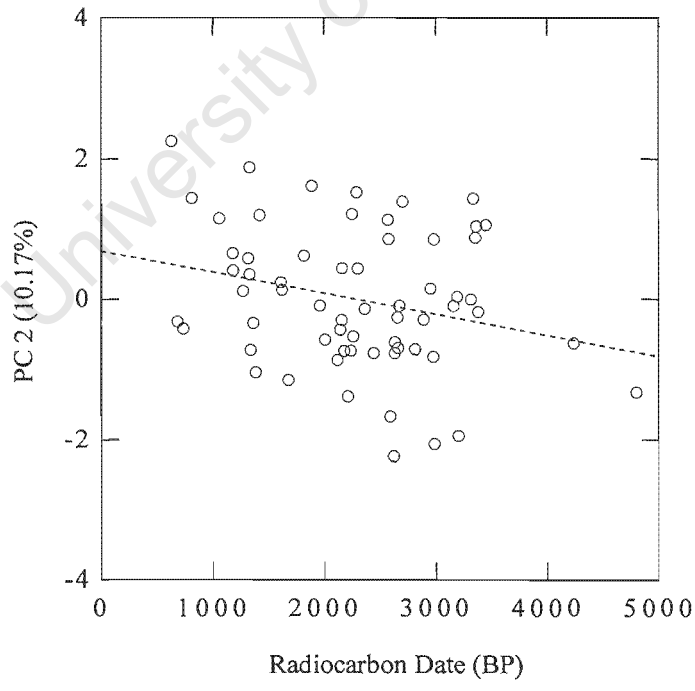

Figure 7.21: Plot of PC 2 of a PCA of all female crania (5000 to 500 BP) against radiocarbon date. Curve represents a linear regression model.

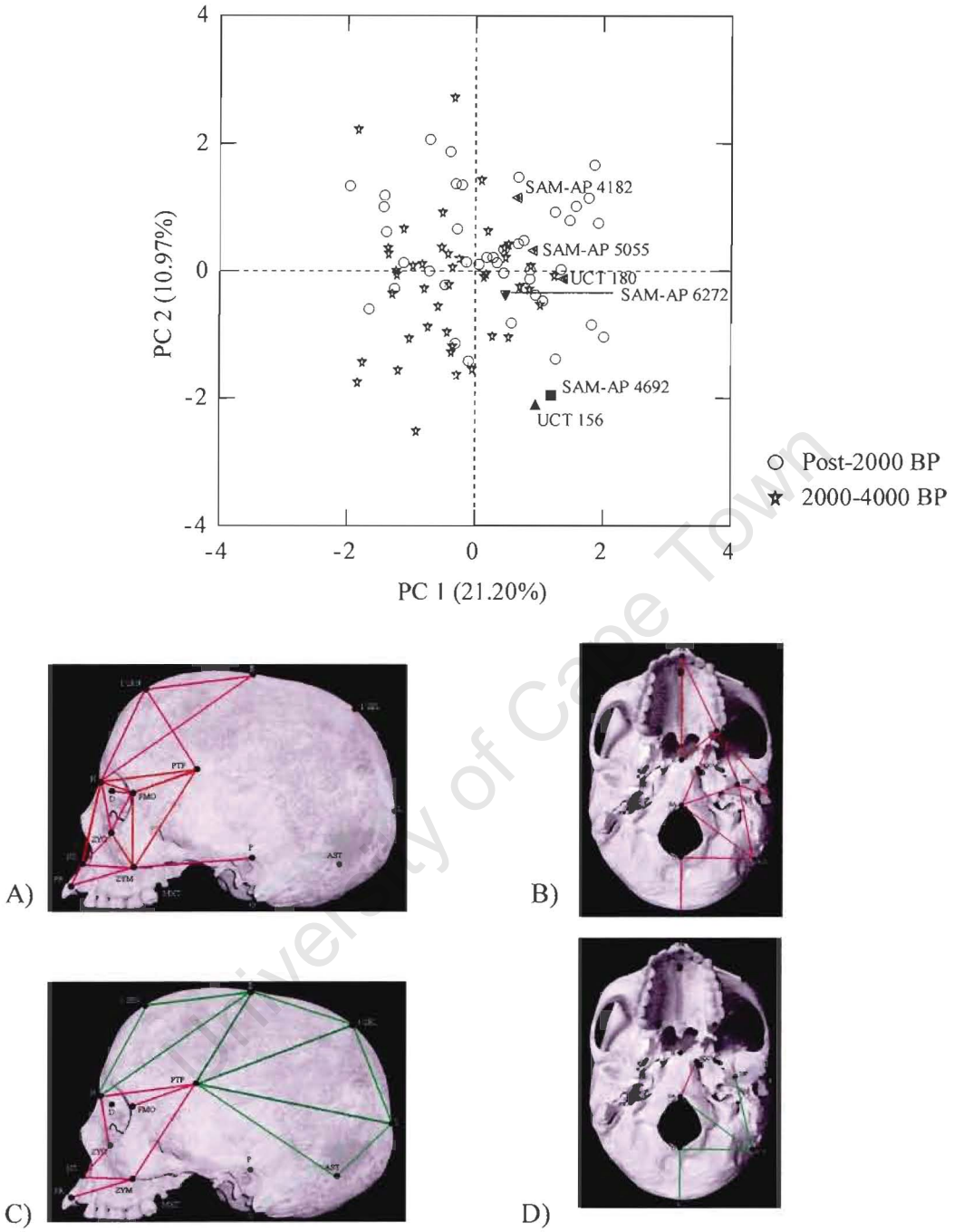

Figure 7.19: Plot of PC 1 and PC 2 of a principal components analysis of all male crania (12000 to 500 BP). Strongly positive and negative loadings on the eigenvectors for PC 1 (A and B) and PC 2 (C and D) are illustrated. Pink represents loadings from 0.1 to 0.19 and blood red represents loadings from 0.2 to 0.29. Light green represents loadings from -0.1 to -0.19, lime green represents loadings from -0.2 to -0.29 and dark green represents loadings below -0.3.

Brown 1987; Lahr and R. V. S. Wright 1996). This phenomenon is investigated for the male Khoesan sample (12 000 – 500 BP) in Figures 7.19 and 7.20. The entire male cranial sample (12 000 – 500 BP) is subjected to a PCA. The variance explained by the PCs with eigenvalues above 1 (fourteen PCs) is presented in Table 7.10. The first fourteen eigenvectors of this PCA is presented in Appendix 13. The loadings of PC 1 and PC 2 in Appendix 13 mirror those of PC 1 and PC 2 in Appendices 5, 8 and 9. PC 1

	Eigenvalue	% of variance	Cumulative %
PC 1	10.18	21.20	21.20
PC 2	5.26	10.97	32.17
PC 3	3.70	7.71	39.88
PC 4	3.21	6.68	46.56
PC 5	2.76	5.74	52.30
PC 6	2.50	5.20	57.50
PC 7	2.33	4.85	62.35
PC 8	1.92	4.00	66.35
PC 9	1.68	3.50	69.85
PC 10	1.54	3.21	73.06
PC 11	1.44	3.00	76.07
PC 12	1.32	2.75	78.82
PC 13	1.24	2.58	81.39
PC 14	1.06	2.20	83.59

Table 7.10: Primary characteristics of the first fourteen principal components of a PCA of all male crania (12 000 – 500 BP).

(21.20%) explains size and size-related shape changes. The most positive values along PC 1 represent crania characterised by long and broad faces, pronounced upper-facial regions and long and broad frontal bones. The most positive values on PC 2 (10.97%) represent crania which exhibit reductions in neurocranial dimensions relative to facial dimensions. As illustrated along PC 1 in Figure 7.19, some of the largest crania in the sample are post-2000 BP crania and crania from the pre-5000 BP sample. In terms of

entire male sample against radiocarbon date. To calculate the allometric shape vector, 45 PCS scores (99.42% of total shape variation) are included in the analysis. The result of the F test for the regression between centroid size and the 45 PCS scores was r^2= 0.68, F= 2.09, p< 0.007, indicating a significant relationship. The plot of the allometric shape vector against radiocarbon date generally mirrors the pattern of male cranial size change during the last 12 000 years (r^2=0.10, F=5.04, p=0.008). At the end of the mid-Holocene, cranial morphology is dominated by short, narrow faces that are retracted in the upper facial region and pronounced in the maxillary region. Frontal regions are steep and neurocrania, particularly in the posterior aspects, are also relatively high at this time. Prior to 5000 BP and after 2000 BP, cranial morphology is dominated by long, broad faces. Upper facial regions are also pronounced, while maxillae are retracted. Frontal regions are lower, as well as posterior neurocranial height. The scale and timing of the shifts in cranial shape are investigated in Figure 7.18. Based on the available data, it appears that cranial shape started changing around 5000 BP, remained relatively stable until 3000 BP, and then started changing again from 3000 BP. As would be expected, this pattern generally follows the pattern of change in cranial size.

OTHER SHAPE CHANGES

Allometric shape changes might explain much of the shape differences between pre-2000 BP and post-2000 BP populations, however, other shape differences also exist. The above analysis shows that there was a gradual reduction in most neurocranial dimensions, relative to facial dimensions, over the last 5000 years. A general reduction in overall neurocranial dimensions is a trend observed in many Holocene human populations (P.

THE TIMING OF ALLOMETRIC SHAPE CHANGE

During the course of evaluating Hypothesis 2, it was determined that cranial size was highest prior to 5000 BP and after 2000 BP. Although it was low between 5000 and 2000 BP, it was at its lowest between 4000 and 3000 BP. This section investigates the timing of allometric shape changes over the last 12 000 years. Only males are investigated since this sample contains individuals older than 5000 BP.

The allometric shape vector is calculated for the entire male sample spanning 12 000 years (Appendix 12). Figure 7.17 presents a plot of the allometric shape vector for the

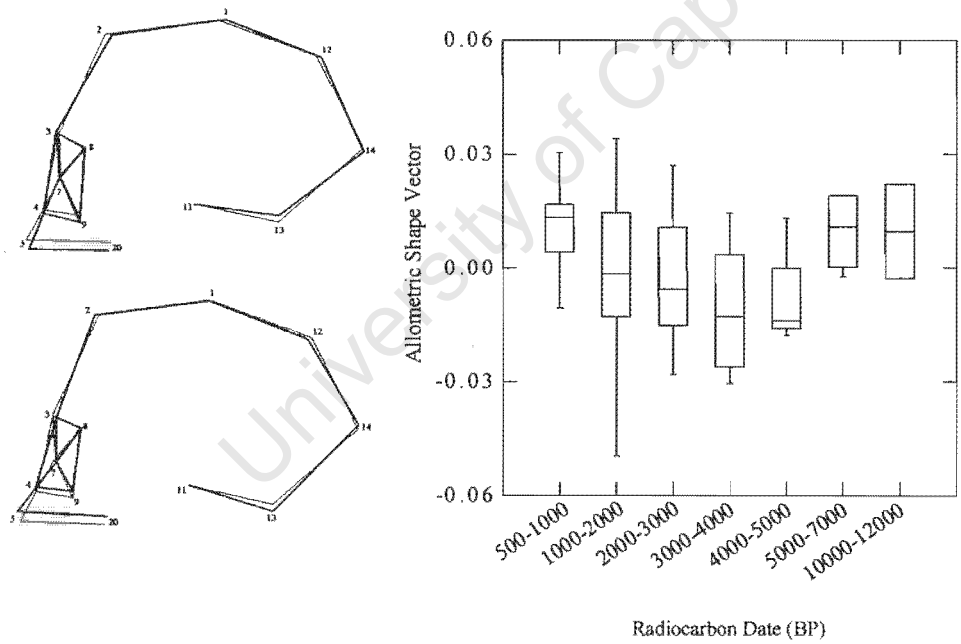

Figure 7.18: Box plots of male allometric shape vector values for the last 12 000 years. The vertical line in the centre of the box marks the median of the sample. The length of each box represents the range within which the central 50% of the values fall, with the box edges at the first and third quartiles. The whiskers extend to the highest and lowest values of the interquartile range. Time is divided into two 2000 year intervals for the pre-5000 BP sample, four one thousand year intervals for the 5000 to 1000 BP sample, and a 500 year interval for the post 1000 BP sample. In the illustrations, grey represents the mean shape, and black, shape change relative to the mean.

backwards. There is a slight decrease in neurocranial height in the posterior aspects of the neurocranium. Crania with the most negative values along the allometric shape vector exhibit a shortening (3-4, 4-5) and narrowing (3-8, 4-9) of the face. At the same time, the maxillary region moves forward (5). The upper-facial region in the area of nasion (3) retracts, while the region midway between the bregma and nasion arc (2) shifts forward, resulting in a steep frontal bone. Neurocranial height increases slightly in the posterior aspects of the neurocranium. The female sample displays a similar pattern of shape differences between crania falling in the positive and negative areas of the plot. Most of the shape changes related to allometry occur in the face. Apart from minor changes in the frontal (most of which is influenced by shifts at nasion) and posterior neurocranial height, the neurocranial shape remains relatively stable between small and large crania.

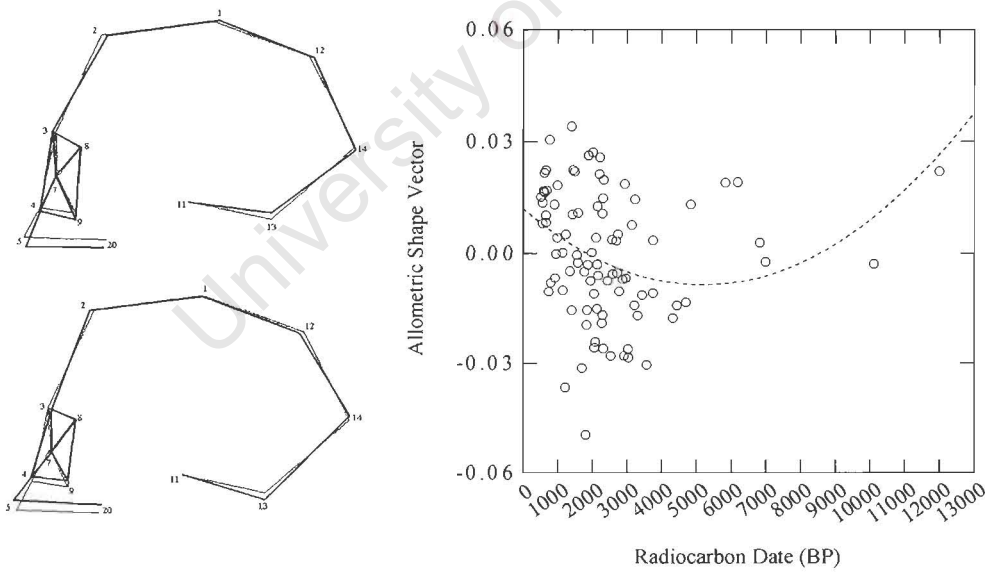

Figure 7.17: Plot of individual male allometric shape vector values (12000 to 500 BP) against radiocarbon date. Curve represents a quadratic regression model. In the illustrations, grey represents the mean shape, and black, shape change relative to the mean.

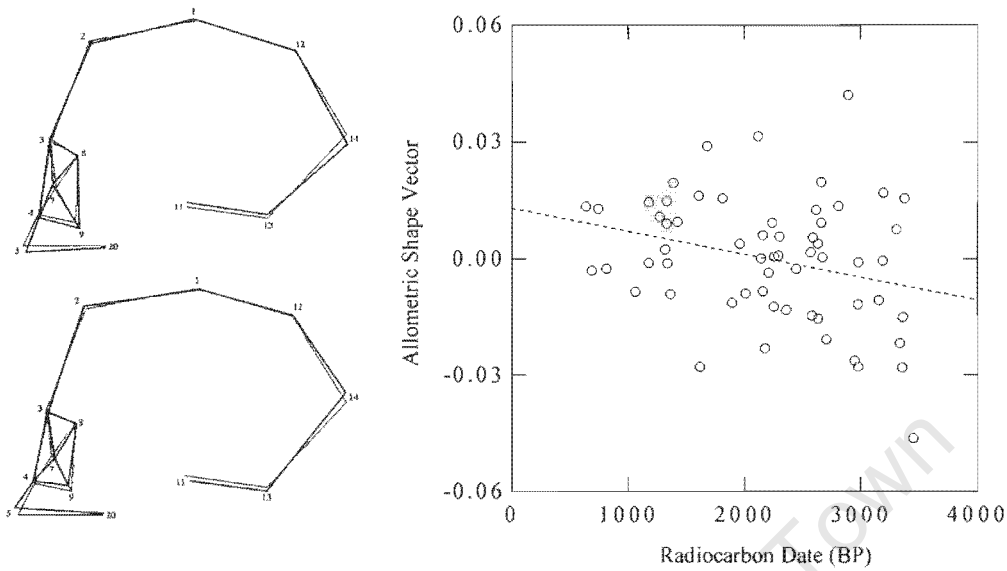

Figure 7.16: Plot of individual female allometric shape vector values for the last 4000 years against radiocarbon date. In the graph, the dashed line represents a linear regression model. In the illustrations, grey represents the mean shape, and black, shape change relative to the mean.

In Figures 7.15 and 7.16, the allometric shape vector is plotted against radiocarbon date for males and females respectively. In both samples, there are gradual increases in allometric shape vector values over the last 3000 years which mirrors the increase in cranial centroid size for this period. The regression statistics for both male (r^2=0.15, F=13.37, p<0.001) and female (r^2=0.08, F=5.07, p=0.03) samples indicate that this linear increase is significant. Shape differences associated with the allometric shape vector are visualized in the sketches adjacent to the graphs. In the case of males, crania with the most positive values along the allometric shape vector are characterised by a significant projection of the upper-facial region in the area of nasion (3), and a reduction in the projection of the frontal bone half way between the bregma and nasion arc (2). These shifts lead to a slightly receding frontal region. In addition to a general lengthening (3-4, 4-5) and widening of the face (3-8, 4-9) the maxillary region also shifts slightly

variation in male and female craniofacial shape during the Holocene is primarily due to allometric scaling.

To start off with, the allometric shape vector is calculated separately for male and female samples spanning the last 4000 years (Appendices 10 and 11 respectively). To calculate the allometric shape vector for the male sample, 40 PCS scores (98.78% of total shape variation) are included in the analysis. The result of the F test for the regression between centroid size (independent variable) and the 40 PCS scores (dependent variable) is significant (r^2= 0.71, F= 2.40, p< 0.003). For the female sample, 29 PCS scores (96.27% of total shape variance) are included in the analysis. The result of the regression between centroid size and the 29 PCS scores is also significant (r^2= 0.68, F= 2.09, p< 0.024).

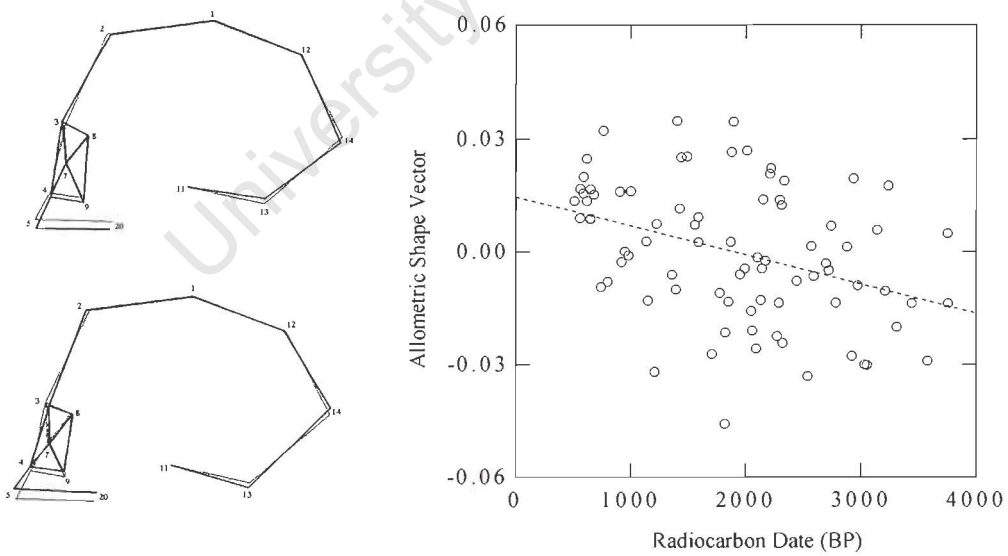

Figure 7.15: Plot of individual male allometric shape vector values for the last 4000 years against radiocarbon date. In the graph, the dashed line represents a linear regression model. In the illustrations, grey represents the mean shape, and black, shape change relative to the mean.

along PC 1 and PC 2 ($p \leq 0.05$). All variables along PC 1 (23%) are positive, indicating that this PC represents overall cranial size and size-related shape. Variables that load particularly high on this PC include those related to facial length and breadth, frontal bone length and overall neurocranial length. On PC 2 (10.17%) the most positive values represent crania which exhibit reductions in neurocranial dimensions relative to facial dimensions. As in the case of the male sample, Figure 7.14 indicates that pre-2000 and post-2000 BP female crania overlap considerably when PC 1 is plotted against PC 2. Nonetheless, it is apparent along PC 1 that overall cranial size increased over the last 2000 years. At the same time, faces became relatively longer and wider, upper facial regions became more prominent, and frontal bones became longer and wider. The location of many post-2000 BP crania along PC 2 indicates that while relative neurocranial dimensions decreased over the last 5000 years, certain facial dimensions, particularly facial and orbit width increased.

ALLOMETRIC SHAPE CHANGE

The above results indicate that size and size-related shape (allometry) are important factors in distinguishing post-2000 BP crania from pre-2000 BP crania. Not only are many post-2000 BP crania large, but they also have longer and wider faces, more prominent upper facial regions, and longer and wider frontal bones than many pre-2000 BP crania. Investigation of Hypothesis 2 has already demonstrated that the increase in cranial size did not start at 2000 BP, but at approximately 3000 BP. This section and the next provide an investigation of the nature of allometric shape changes during the Holocene. It thus sets out to evaluate Sub-hypotheses 3e and 3f which state that the major

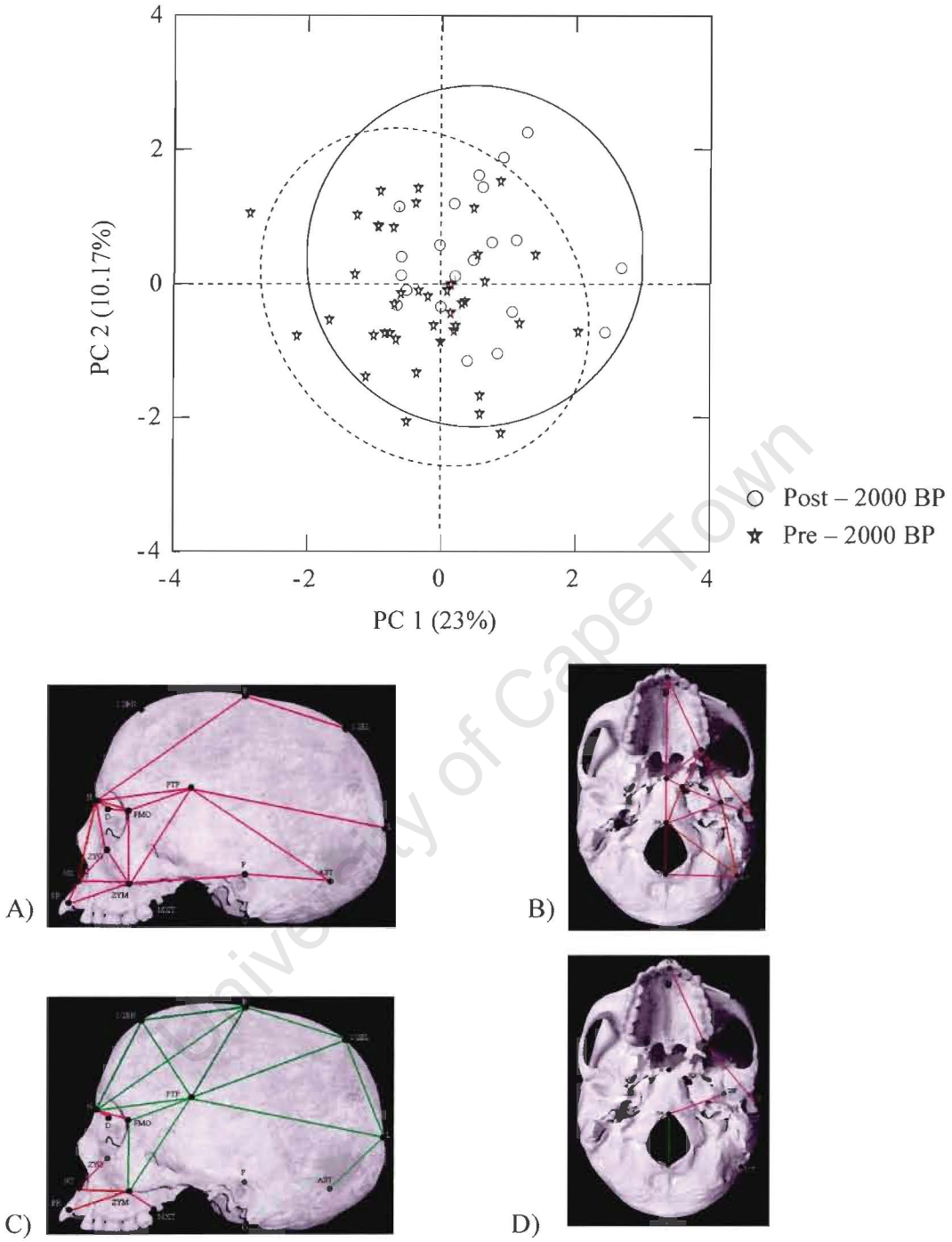

Figure 7.14: Plot of PC 1 and PC 2 of a principal components analysis of post-5000 BP female crania. Strongly positive and negative loadings on the eigenvectors for PC 1 (A and B) and PC 2 (C and D) are illustrated. Pink represents loadings from 0.1 to 0.19 and blood red represents loadings from 0.2 to 0.29. Light green represents loadings from -0.1 to -0.19, lime green represents loadings from -0.2 to -0.29 and dark green represents loadings below -0.3.

	df	F	Significance (p=0.05)
PC1	1	**8.71**	0.00
PC2	1	**5.64**	0.02
PC3	1	3.37	0.07
PC4	1	0.54	0.46
PC5	1	1.15	0.29
PC6	1	1.56	0.22
PC7	1	0.20	0.65
PC8	1	1.04	0.31
PC9	1	1.57	0.21
PC10	1	0.22	0.64
PC11	1	0.33	0.57
PC12	1	0.00	0.94
PC13	1	2.15	0.15
PC14	1	0.06	0.80

Table 7.8: Results of an analysis of variance (ANOVA) performed on the first fourteen PCs of a PCA of post-5000 BP female crania.

	Eigenvalue	% of Variance	Cumulative %
PC1	11.04	23.00	23.00
PC2	4.88	10.17	33.17
PC3	4.07	8.49	41.66
PC4	3.26	6.80	48.46
PC5	3.08	6.42	54.88
PC6	2.44	5.09	59.97
PC7	2.29	4.78	64.75
PC8	1.88	3.92	68.68
PC9	1.65	3.45	72.12
PC10	1.47	3.07	75.19
PC11	1.40	2.92	78.12
PC12	1.35	2.80	80.92
PC13	1.23	2.56	83.48
PC14	1.01	2.11	85.59

Table 7.9: Primary characteristics of the first fourteen principal components of a PCA of post-5000 BP female crania.

In the case of the female sample, Table 7.8 presents the results of an ANOVA performed on the eigenvalues greater than one. The variance explained by the first 14 PCs is presented in Table 7.9. Appendix 9 presents the eigenvectors for the first 14 PCs. Pre-2000 BP and post-2000 BP samples were significantly different from one another only

and Singer 1967; Rightmire 1970; Hausman 1980). There is however little basis for claiming that cranial size or any other cranial trait mentioned in previous literature could successfully discriminate between San and Khoekhoe crania. For much of the history of South African physical anthropology, there had not been a clear definition of the biological or cultural traits which distinguish the San from the Khoekhoe (Tobias 1978). When assembling cranial samples for analyses, different researchers often employed widely divergent criteria to identify San and Khoekhoe crania. For this reason, much of the published data on cranial differences between the San and Khoekhoe is unreliable. Nevertheless, early characterisations continued to influence research into Khoesan biological evolution prior to the wide scale availability of radiocarbon dating. Since large size and robusticity was widely regarded as a Khoekhoen trait, large crania of unknown origin were routinely assigned to the Khoekhoe. Alternatively, small, gracile crania of unknown origin were assigned to the San. This was not always correct. For instance, Rightmire (1970) and Hausman (1980) suggested that two large undated crania from the site of Oakhurst, UCT 180 and UCT 192, significantly resembled the crania of recent Khoekhoe herders, and were probably Khoekhoe. These two crania were subsequently dated to the mid-Holocene (Patrick 1989); an unexpected result that suggests that large, robust cranial morphology may have greater antiquity. However, the lack of a well-dated cranial series made it practically impossible for researchers to study Khoesan morphological trends through the Holocene.

With an increase in the availability of dated cranial material during the late 1980's and 1990's, the original picture of Khoesan evolutionary development during the Holocene

started to change. Based on a small sample of mostly fragmentary cranial material dated to the early to mid-Holocene, Bräuer and Rösing (1989) were able to demonstrate that large, robust cranial morphology was already present in South African human populations during the early Holocene.

Interestingly, some early researchers had commented on the existence of large, robust crania in early archaeological deposits prior to the availability of direct dating methods (Dreyer 1933; Hoffman 1958; Louw 1960). Although excavation methods were very crude and the stratigraphic provenances of individual fossils were in many cases uncertain, these researchers noted further that small, gracile crania were absent in older deposits, and only emerged later in the sequence after which they then co-occurred with large, robust crania. An early theory suggested that the small, gracile crania belonged to the ancestors of recent Bush (San) peoples who migrated into the region, while the large, robust crania belonged to indigenous "Boskopoid" people. In addition to co-existing throughout history as separate forms, these two forms also supposedly interbred, leading to Bush-Boskop or Boskop-Bush hybrids (Laing 1924; Galloway 1937b). Drennan (1938) even argued that the origins of the Khoekhoe herders may be attributed to hybridisation between Bush and Boskop populations.

The results of the current analysis confirm that the South African Holocene human cranial record is indeed variable; however the level of variability is quite subtle. These

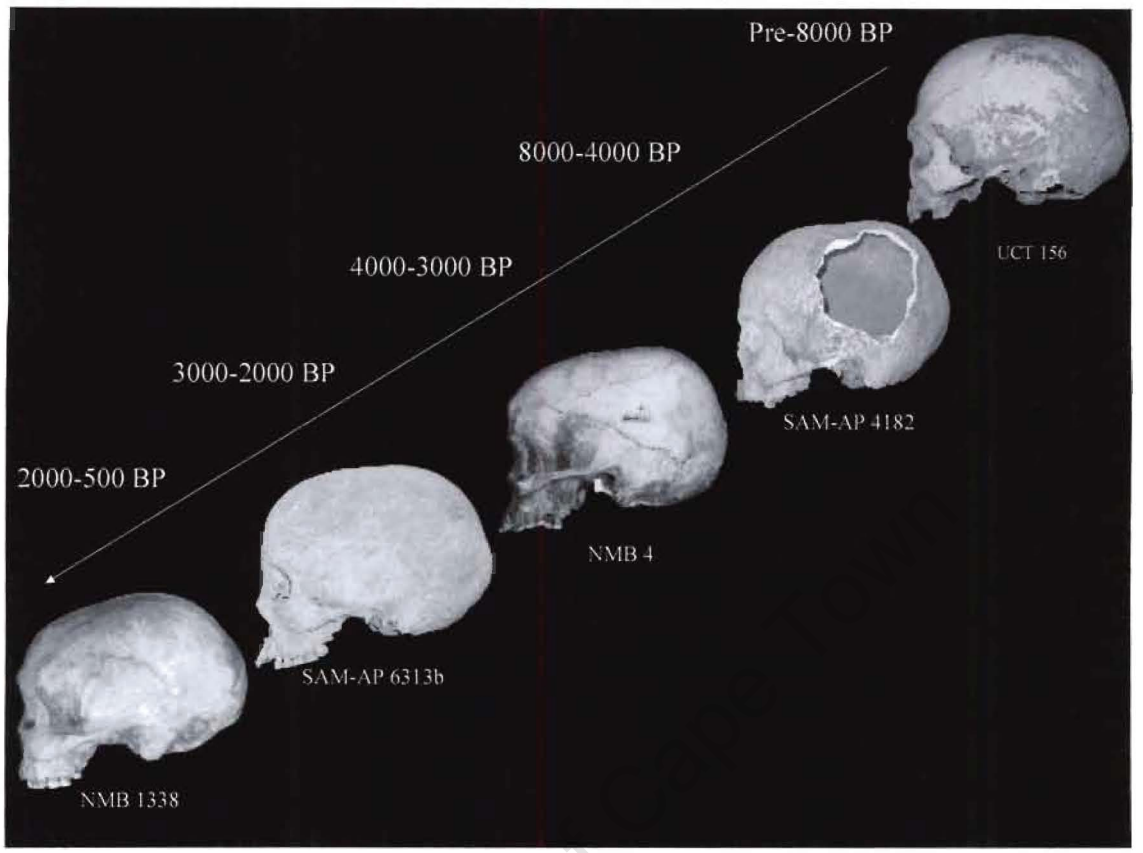

Figure 8.1: Five morphotypes (all male) of different radiocarbon age which summarise the primary craniofacial change in South African Holocene populations. Specimens were chosen for illustration as being closest to the group centroid.

results also provide the first evidence that a significant temporal aspect is involved in this variation. Figure 8.1 displays five morphotypes which summarise the primary craniofacial change in South African Holocene populations. Consistent with the results of Bräuer and Rösing (1989), early to mid-Holocene populations are characterised by large, robust crania. Supraorbital regions are robust and particularly pronounced, while frontal bones recede. Upper faces project slightly compared to maxillary regions and are long and broad. Faces are generally robust. Neurocrania are large, relative to facial dimensions. Between 4000 and 3000 BP, there is a general decline in cranial size and robusticity, as well as allometric shape changes in the face and frontal bone. Supraorbital regions are

gracile and retracted, while frontal bones are steep and prominent. Upper-facial regions are orthognathic, while maxillary regions project slightly. Upper-faces are short and narrow. Neurocrania remain large relative to facial dimensions. Craniofacial form did not remain small and gracile though. In contrast to the suggestions of Bräuer and Rösing (1989), there is a general recovery in craniofacial size and robusticity levels from 3000 BP which extends into the last 2000 years. Upper-facial regions again become pronounced and frontal regions recede. Faces become large and robust. Unlike preceding populations though, neurocranial dimensions decrease relative to facial dimensions. Interestingly, neurocranial shape remains dolichocephalic throughout the Holocene despite reductions in size.

These results, like those of Bräuer and Rösing (1989), highlight the shortcomings of previous research which placed strong emphasis on the premise that large, robust crania belonged to Khoekhoe individuals and as such dated to the last 2000 years. They also contradict suggestions that small, gracile cranial morphology was the dominant form during much of the Holocene. The opposite is in fact true. Large, robust crania dominate for much of the Holocene, while small, gracile crania are dominant only between 4000 and 3000 BP, after which they become progressively rarer again. These results thus raise serious questions about the conclusions of previous research on the evolution of the Khoesan during the Holocene, particularly regarding the issue of separate Khoekhoe and San populations. As such, it places renewed emphasis on the need to reinvestigate the implications of craniofacial variability in South African LSA populations.

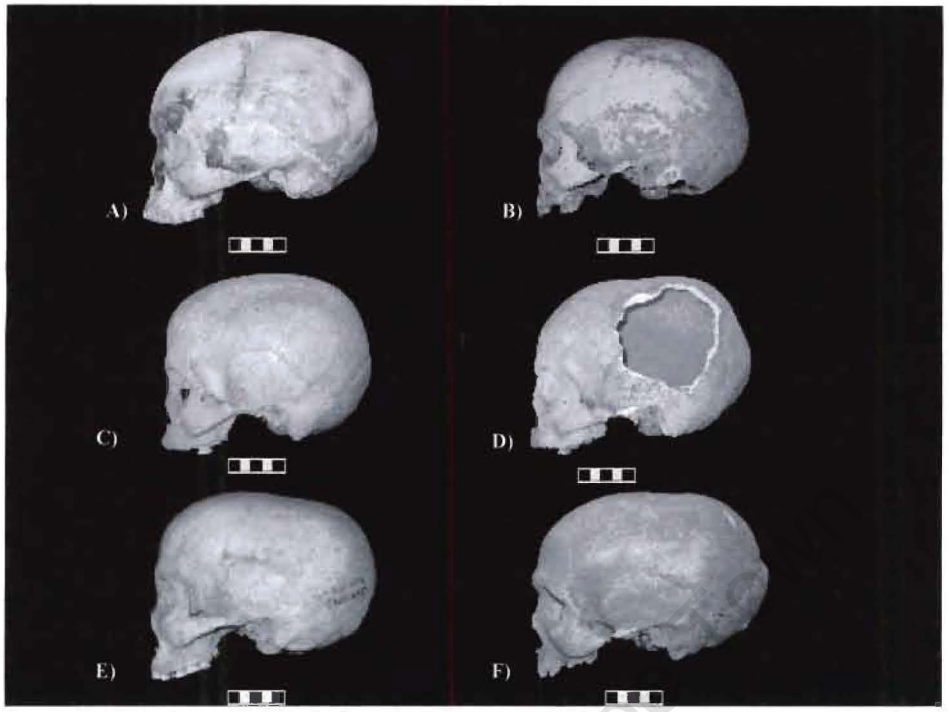

Figure 8.2: Lateral views of pre 5000 BP crania analysed in this study.
A) SAM-AP 4692; B) UCT 156; C) SAM-AP 5055; D) SAM-AP 4182; E) UCT 180; F) SAM-AP 6272.

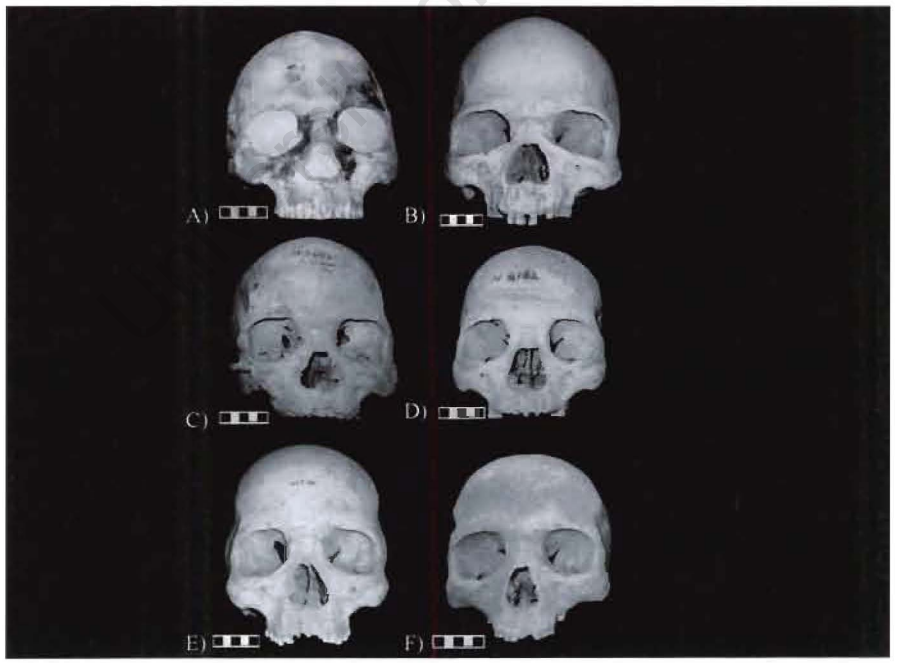

Figure 8.3: Anterior views of pre 5000 BP crania analysed in this study.
A) SAM-AP 4692; B) UCT 156; C) SAM-AP 5055; D) SAM-AP 4182; E) UCT 180; F) SAM-AP 6272.

THE ORIGINS OF KHOESAN CRANIOFACIAL MORPHOLOGY

Genetic evidence indicates that sub-Saharan African populations and the Khoesan in particular, possess some of the deepest genetic roots of all recent humans. Although some have claimed that Khoesan morphology is also quite ancient (Tobias 1964, 1978), this claim has not stood up to scrutiny of the fossil record. Late Pleistocene South African fossils such as Klasies River, Border Cave and Hofmeyr are morphologically distinct from recent Khoesan populations. The first appearance of typical Khoesan craniofacial morphology occurred in terminal Pleistocene/early Holocene populations (Rightmire 1974, 1978b; Braüer and Rösing 1989). This study confirms that the craniofacial morphology of these early terminal Pleistocene/early Holocene populations resembles later Khoesan populations. Analyses carried out on six complete crania dating to between *ca.* 12 000 and 5000 BP (Figures 8.2 and 8.3) indicate that these terminal Pleistocene/early Holocene crania fall within the range of variation of a large sample of recent Khoesan crania. In the most recently published analysis of South African human crania from the early Holocene, Bräuer and Rösing (1989) pointed out that these early populations closely resemble later populations in terms of facial shape, but were markedly larger, particularly with respect to neurocranial dimensions, and generally more robust, than the crania of later populations (Bräuer and Rösing 1989). In accordance with the observations of Bräuer and Rösing (1989), the current study demonstrates that early crania possess the euryprosopic facial shape typical of recent Khoesan crania (Figure 8.3). At the same time, overall cranial size in the early sample is large. The earliest crania, SAM 4692 and UCT 156, possess neurocrania that are among the largest in the studied sample. Neurocranial shape in the pre-5000 BP sample is overwhelmingly

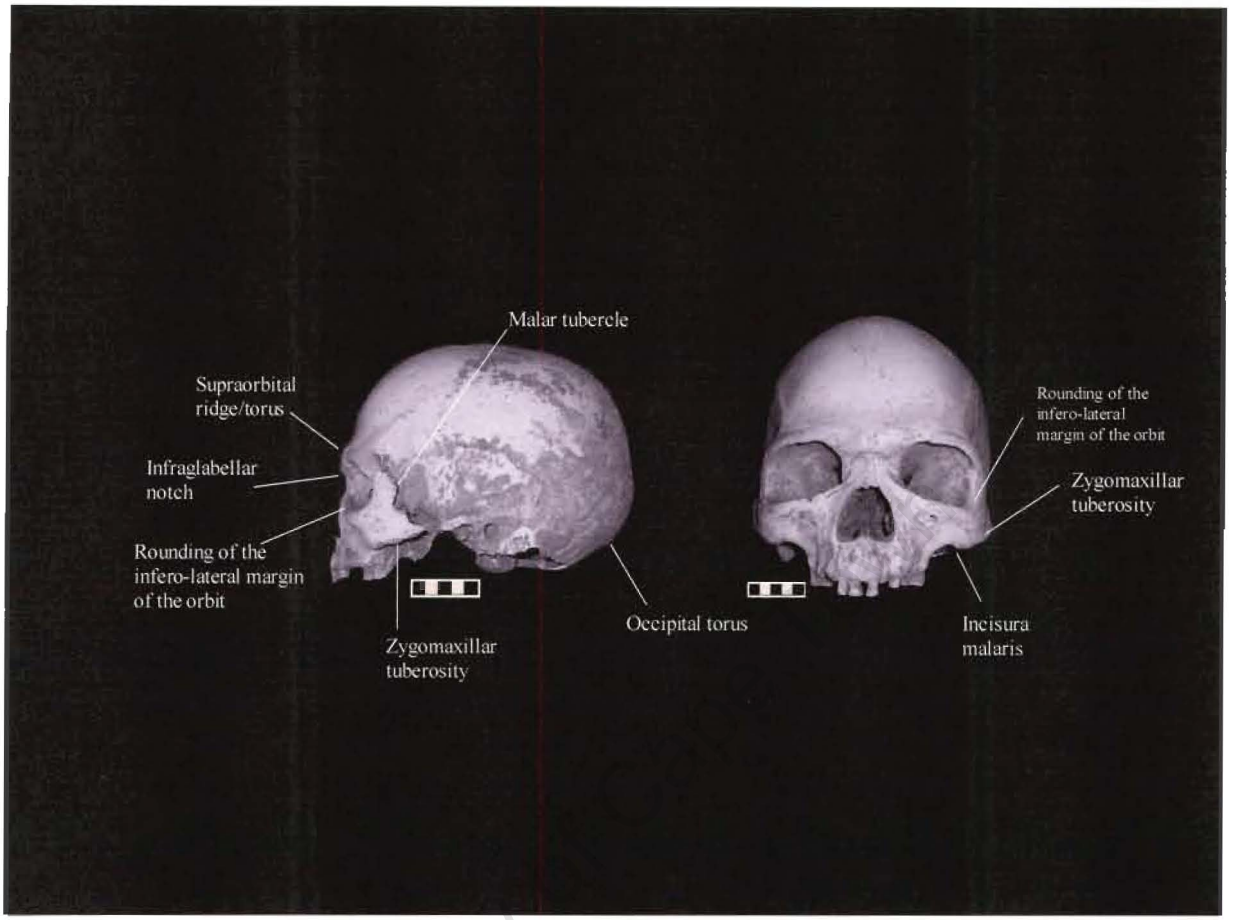

Figure 8.4: Features of robusticity (as per Lahr 1996) present on UCT 156.

dolichocephalic (Figure 8.2). Not only are these early crania large, but they are also robust. A visual inspection indicates that supraorbital regions are pronounced, zygomaxillary tuberosities and zygomatic trigones are well-developed, and muscle attachments in the occipital regions are marked (Figure 8.4). Although this study confirms that terminal Pleistocene/early Holocene crania are large and robust, it contradicts Bräuer and Rösing's (1989) assertion that these early crania are significantly larger and more robust than later crania. There are some crania in the post-2000 BP sample that are even larger and more robust than these early crania. What is evident though is the absence of small, gracile crania in the early sample. The contradiction

between the results of this study and that of Bräuer and Rösing's (1989) can probably be attributed to sample size. Unlike Bräuer and Rösing's (1989) study, this study had access to a large sample of dated crania which allowed for a more accurate comparison between the craniofacial morphology of early and later populations.

Despite their diverse geographic origins and great temporal span, Mahalanobis distances indicate that the six pre-5000 BP crania are relatively homogenous and display a level of inter-individual variation that is consistent with crania originating from a single biological population. The morphological similarity between the pre-5000 BP crania and more recent crania, together with the high level of homogeneity displayed by crania in the pre-5000 BP sample, is consistent with A. G. Morris' (2002, 2003) hypothesis that Khoesan morphology developed in a geographically isolated South African population during the LGM. Glacial periods, which promote an increase in arid conditions and an increase in the ice-caps, are suspected of having played a major role in the isolation of human populations during the Pleistocene (Sarich 1997; Lahr and Foley 1998). Under glacial conditions, gene flow between populations would have been restricted. Instead, genetic drift, and in certain cases, natural selection, would have had important influences on the overall phenotype and genotype of human populations. A lack of gene flow, combined with an increase in genetic drift and natural selection in isolated human populations, would have reduced homogeneity across populations and led to differentiation between populations (Relethford 2001a, 2004). The South African fossil record appears to bear this out. As mentioned, South African human fossils pre-dating the LGM (e.g. Klasies River, Border Cave and Hofmeyr) are characterised by a generalised

African craniofacial morphology (de Villiers 1973; Ambergen and Schaafsma 1984; Van Vark 1986; A. G. Morris and Grine 1999; A. G. Morris *et al.* 2005). This is consistent with the existence of genetic links between southern African populations and populations further north. Shortly after the LGM though, craniofacial morphology which can be considered typically Khoesan, appear in the South African fossil human record (e.g. the terminal Pleistocene Fish Hoek cranium). The uniqueness of this craniofacial morphology to the region is confirmed by a lack of human fossils displaying unambiguously Khoesan craniofacial morphology north of the Cunene and Zambezi rivers (A. G. Morris 2002). The Khoesan thus appears to have remained a strictly regional phenomenon since their origin in southern Africa during the terminal Pleistocene.

In terms of their large overall size, robusticity and dolichocephalic neurocranial shape, pre-5000 BP South African crania mirror a morphological pattern exhibited by many other late Pleistocene/early Holocene human populations around the world. However, in contrast to the skeletal records of Europe, Asia and the Americas, these early South African crania are not morphologically distinct from more recent Khoesan crania. Instead, the Khoesan fossil record broadly mirrors that of the Australian Aborigines, a population that was isolated from early Holocene agricultural developments and human migrations. The general craniofacial pattern (*bau plan*) exhibited by contemporary Australian Aborigines resembles that of Late Pleistocene populations to a large extent. Their crania are however slightly smaller than those of their Late Pleistocene predecessors, the result of a decline in cranial size that occurred between 8000 and 6000 BP (P. Brown 1987, 1992).

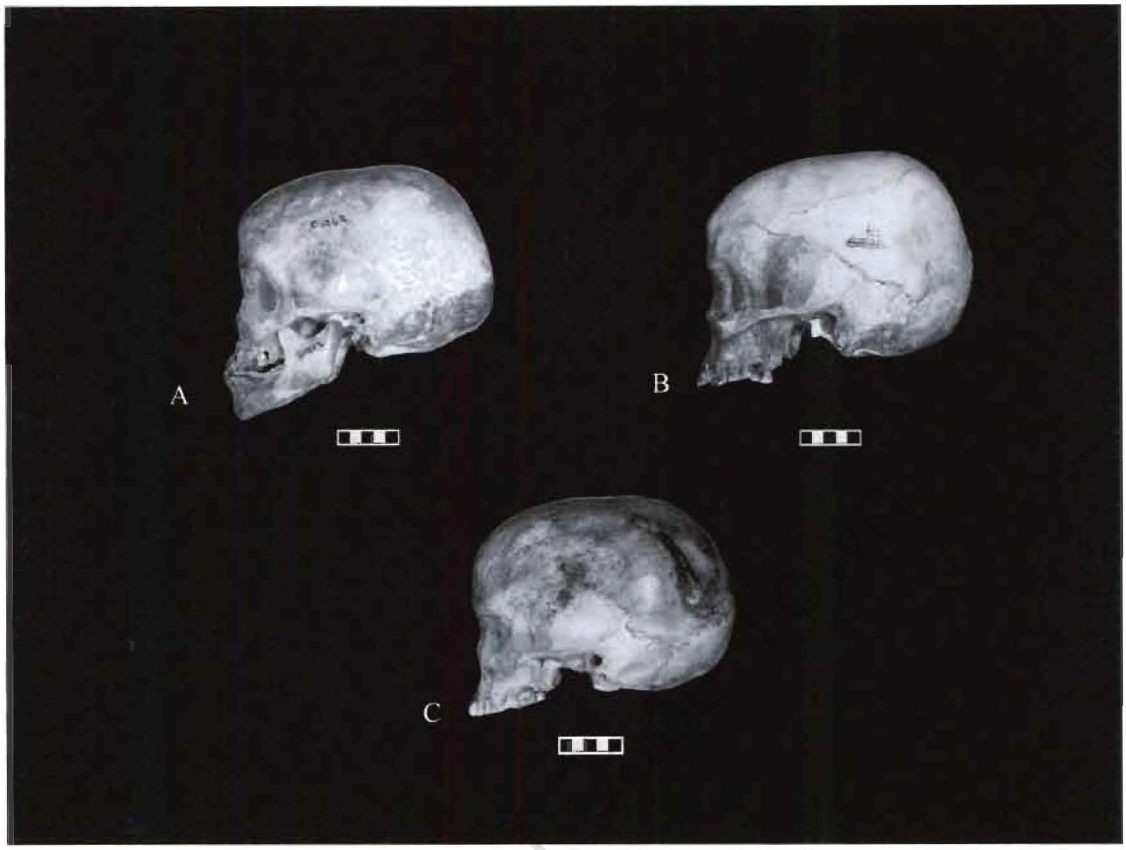

Figure 8.5: Lateral views of 3 crania (male) from the 4000 – 3000 BP period.
A) NMB 1242; B) NMB 4; C) NMB 1273. Specimens were chosen for illustration as being closest to the group centroid.

LATE MID-HOLOCENE FLUCTUATIONS IN KHOESAN CRANIAL SIZE

Between approximately 4000 and 3000 BP, populations in the Fynbos Biome exhibit dramatic reductions in stature (Pfeiffer and Sealy 2006). At the same time, there is a reduction in overall cranial size and accompanying size-related shape changes which primarily affect the viscerocranium and frontal region. Cranial shape is characterised by non-projecting upper-facial regions; faces that are relatively short and narrow; frontal bones that are short and narrow, but steep (Figure 8.5). There is also a marked reduction in overall cranial robusticity (as represented by the gracilisation of features described in Figure 8.4). The supraorbital and zygomatic regions are particularly lightly developed.

The fact that there is a simultaneous reduction in post-cranial and cranial size suggests that there is a general reduction in body dimensions at this time. However, the specific causes of this reduction are not clear. Reductions in body size occurred after the early to early mid-Holocene increase in temperature (*ca.* 8000 BP – 6000 BP). An increase in climatic conditions therefore could not have been responsible for the observed changes in craniofacial form. Changes in craniofacial form also occurred prior to the introduction of pastoralism, farming and pottery vessels to the region (*ca.* 2000 BP). Since the types of food available to people and the method of food preparation remained relatively unchanged for the Holocene prior to 2000 BP (i.e. hunting and gathering), biomechanical changes associated with alterations in diet can also not explain the changes in craniofacial form. A lack of large scale cultural change between 4000 and 3000 BP largely precludes the genetic influence of a migrant population (J. Deacon 1984a). There is also very little evidence of widespread infectious disease which could have restricted growth at this time (Pfeiffer 2002; Pfeiffer and Crowder 2004). According to Pfeiffer and Sealy (2006), the most likely cause may be chronic and/or cyclical insufficiency of nutrients, an argument supported in this thesis.

A dramatic increase in archaeological sites along the South African coast as well as inland during the latter half of the Holocene (post-Classic Wilton), suggests significant population growth in the region. This increase in population may have restricted mobility (Sealy and Pfeiffer 2000) and placed tremendous stress on natural resources, leading to seasonal shortages. To overcome this, people started exploiting a wider range of foods. This process of resource intensification is best documented in the densely occupied Cape

Ecozone and Thukela Basin in KwaZulu-Natal (Hall 1990; Mazel 1989). In other parts of the world such as the Near East, similar processes of resource intensification had led to the emergence of agriculture during the early Holocene (Bar-Yosef and Meadow 1995). The process of mid- to late Holocene intensification in the Fynbos Biome and other regions of the subcontinent did not result in the emergence of local forms of agriculture. Instead, the domestic animals associated with pastoralism and the crops associated with farming in South Africa had their origins in regions further north in the continent, and/or in other continents (Wendorf and Schild 1994). These subsistence strategies only became a factor in the South African social and economic landscape after *ca.* 2000 BP. Population growth and resource intensification may not have led to the development of local forms of agriculture, nevertheless, there appear to have been significant changes in social and economic relationships amongst resident groups, as suggested by the archaeological record. Concomitant reductions in overall body size and changes in cranial shape suggest that the population may also have been under greater nutritional stress (because of an increase in population density and resulting food shortages) than at any other time during the Holocene.

According to Steckel *et al.* (2002) acute food shortage may inhibit long bone growth in children, preventing them from reaching their full growth potential. As a result, adults that had experienced malnutrition during childhood would exhibit shorter than normal stature levels and increased gracility of the post-cranial bones. The effects of dietary constraints on the craniofacial skeleton are more complex. Analyses carried out on the crania of non-human primates (Pucciarelli *et al.* 1990, 2000; Pucciarelli and Dressino

1996; Dressino and Pucciarelli 1997, 1999; Cónsole *et al.* 2001) and rats (Pucciarelli 1980, 1981; Engstrom *et al.* 1982; Pucciarelli and Goya 1983; Pucciarelli *et al.* 1984; J. P. Miller and German 1999) that had been malnourished as juveniles, indicate that malnutrition delays growth in cranial size and changes craniofacial shape. Malnutrition appears to affect craniofacial shape and size in a predictable manner regardless of the species differences. The regions that are most affected are also those with the greatest growth rates, namely regions of the viscerocranium. In particular, the masticatory and respiratory regions, display the greatest growth arrest. In terms of shape, masticatory and respiratory regions exhibit reductions in length while widths are less affected. On the other hand, the neurocranium which grows more slowly and for a longer period, is relatively stable (Dressino and Pucciarelli 1997, 1999; J. P. Miller and German 1999). Although the neurocranium is relatively stable even under times of dietary constraints, anterior and middle neural regions display slight reductions in length, while width is relatively unaffected. Neurocranial shape is also linked to the growth of the brain and is therefore less affected by environmental factors such as dietary constraints (Wood and Lieberman 2001).

The reductions in craniofacial size and patterns of craniofacial shape change observed in Khoesan crania between 4000 and 3000 BP mirror the pattern of morphological change which would be expected in individuals that had experienced dietary constraints as juveniles. While relative neurocranial dimensions remain comparatively stable, there are marked reductions in most dimensions of the viscerocranium, particularly reductions in lengths. Consequently, facial regions are small and retracted. The retraction of the face

would in turn explain reductions in the supraorbital region and also the steeper frontal regions of crania at this time. According to Lieberman (2000) and Lieberman *et al.* (2002), primates with retracted faces have reduced supraorbital regions and steeper frontal regions, reflecting the supraorbital region's role to integrate spatially the upper face and the neurocranium. The lack of any substantial change in the neurocranium and basicranium, two regions with high levels of heritability, is consistent with genetic continuity in the population at this time.

In contrast to genetic changes in a population, changes due to environmental factors may subsequently exhibit a reversal. Ruff *et al.* (1997) and Katzmarzyk and Leonard (1998) note that some post-Neolithic populations living in higher latitudes that had undergone reduction in body size during the early Holocene display a reversal in low stature levels during the latter half of the Holocene. On the other hand, stature levels remained low in lower-latitude populations with the exception of some very recent increases (Katzmarzyk and Leonard 1998). As with the initial reductions in stature, the recent increases in stature in higher latitude populations are thought to be linked to an improvement in nutritional and health levels (Van Wieringen 1986; Eveleth 1994; Ruff 2002). A similar recovery in stature is observed in the Khoesan. Although the Khoesan are a low-latitude population, Pfeiffer and Sealy (2006) recorded a recovery in stature levels which started at *ca.* 3000 BP. A concurrent recovery in size occurred in the craniofacial skeleton, strengthening the argument that the late mid-Holocene reduction in Khoesan cranial size was due to environmental factors and not due to genetic changes in the population. Earlier studies, based on a smaller skeletal sample, have argued that South African Khoesan populations

displayed an increase in stature at 2000 BP. This increase, it was further argued, was related to gene flow from immigrant herders into the region (P. Smith *et al.* 1992; Wilson and Lundy 1994). However, as Pfeiffer and Sealy's (2006) study has shown, this increase in stature began at *ca.* 3000 BP, a millennium before domestic stock appeared in the South African archaeological record. It thus cannot be linked to the migration of herders. Instead, Pfeiffer and Sealy (2006) have argued that the observed increase in stature may be attributed to people solving nutritional problems within a hunter-gatherer economy.

THE INTRODUCTION OF PASTORALISM AND POPULATION CONTINUITY

The question of population continuity between pre-herder and post-herder time periods is an important issue in South African anthropology. Archaeological evidence has revealed that herding was introduced to South Africa at *ca.* 2000 BP. Until now, however, archaeological and biological research has been unable to determine conclusively whether the introduction of domesticates was facilitated by the migration of biologically distinct herders from further north in the continent, or whether herding entered the region via the acculturation of local hunter-gatherers.

Results presented in this thesis indicate that although there was a minor, but significant increase in inter-individual morphological distances in post-2000 BP crania compared to pre-2000 BP crania, this was not due to the inclusion of morphologically distinct individuals. Neither was there a major change in human craniofacial form in the research region at 2000 BP. This is significant, because much of the evidence for herding comes

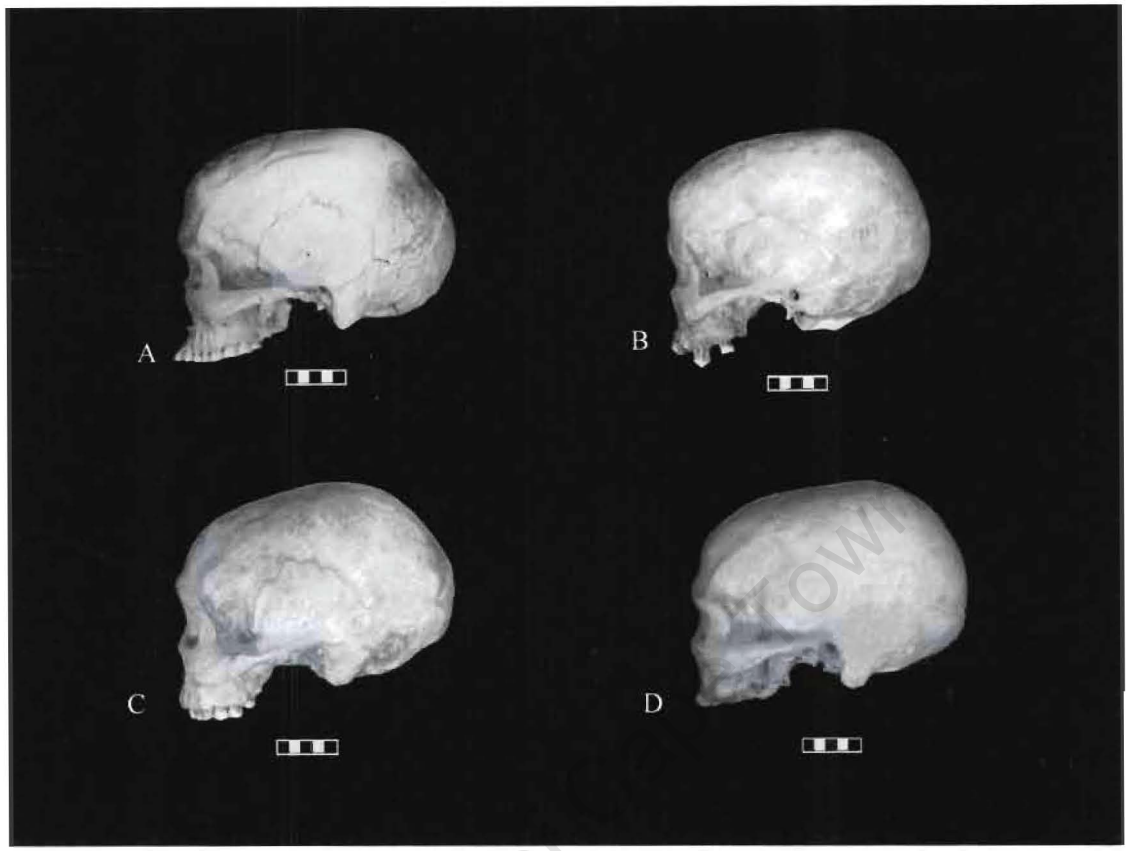

Figure 8.6: Lateral views of 4 crania (male) from the post-2000 BP period.
A) NMB 83; B) NMB 1707; C) NMB 1338; D) NMB 1207. Specimens were chosen for illustration as being closest to the group centroid.

from archaeological sites in the coastal region. If herding was introduced by the migration of biologically distinct populations, one may expect to see a significant change in craniofacial form at around 2000 BP. This result is in accordance with the findings of Hausman (1980) who also found little craniofacial variation in her coastal cranial sample. Although there was not a sudden change in craniofacial morphology at 2000 BP, data presented in this thesis indicate that post-2000 BP populations do display a general increase in cranial size relative to most pre-2000 BP crania. However, results suggest that the generally larger size of post-2000 BP crania was not due to any biological change that occurred within the last 2000 years, but instead reflects the culmination of a recovery in

cranial size that began at 3000 BP. At the same time, craniofacial shape characterised by non-projecting upper-facial regions, relatively short and narrow faces and steep frontal regions, were gradually replaced by more robust morphologies characterised by projecting upper-facial regions, long and broad faces and low frontal regions (Figure 8.6). As discussed above, the shape changes which affect mainly the face and frontal region are allometric in nature and related to the recovery in cranial size at 3000 BP.

In addition to the aforementioned changes in cranial form, post-2000 BP crania also display reductions in neurocranial dimensions relative to facial dimensions, when compared to pre-2000 BP crania. These reductions in relative neurocranial dimensions did not commence at 2000 BP though, but can be traced back to at least the early Holocene. They are therefore also unrelated to the mid-Holocene reduction in cranial size. The cause of these neurocranial reductions is difficult to pinpoint since they appear to have their origins prior to the Holocene. Evidence from other populations may shed some light on this issue though, since similar reductions in relative neurocranal dimensions have been recorded for many other human populations around the globe during the same period (Henneberg 1988; Henneberg and Steyn 1993; Grimaud-Hervé 1997). An analysis of neurocranial dimensions in Late Pleistocene and Holocene populations indicate that there had been a gradual reduction in human cranial capacity since the Mesolithic in Europe and the Middle Stone Age in Africa (Henneberg 1988; Henneberg and Steyn 1993). The decrease in cranial capacity in Europe, Asia and the Americas was also accompanied by gradual brachycephalization. In sub-Saharan Africa, reductions in cranial capacity were not accompanied by brachycephalization, and neurocranial shape

generally remained dolichocephalic. This pattern of neurocranial change is also apparent in the Khoesan sample analysed in this thesis. Although this sample exhibits reductions in neurocranial dimensions during the course of the Holocene, the majority of neurocranial dimensions are affected. Neurocranial shape thus remains dolichocephalic. It has been noted that reductions in neurocranial dimensions are part of a general reduction in human body mass, skeletal size and robusticity during the last 50 000 years (Frayer 1980, 1984; Henneberg 1988; P. Brown 1992; Henneberg and Steyn 1993; Ruff 2002). Currently, very little is known about the causes of this reduction. Some have suggested that it was related to a reduced selection for large body size due to technological improvements (Frayer 1984). Others have argued that selection for smaller body size may have been driven by a wider array of factors, which, in addition to technological improvements, also included social, behavioural and cultural modernisation. Together, the effects of these changes may have lead to humans essentially domesticating themselves via a process of "unconscious selection" (Leach 2003). It has been noted that humans display many similar morphological changes to animals that had been domesticated, including a decrease in brain size (Leach 2003; Kruska 2005). Whatever the cause of the reduction in cranial capacity may have been, it is significant that it has also now been recorded in the Khoesan.

As mentioned in Chapter 1, expedition diaries from the early colonial period comment extensively on the socio-economic conditions and physical appearances of hunter-gatherer and herder bands. The San were often described as tiny, while the Khoekhoe pastoralists were described as tall (Thom 1958). These descriptions of stature differences

mirror the results of previous physical anthropological studies which characterise the crania of San hunter-gatherers as small and gracile and those of Khoekhoe herders as large and robust. If these early accounts are accepted as accurate, and these physical differences actually existed between the practitioners of the two life ways, gene flow into the region at 2000 BP is unlikely to account for the origins of the Khoekhoe. As demonstrated in this thesis, the lack of a significant change in craniofacial morphology at 2000 BP undermines hypotheses postulating that recent Khoekhoe populations were the descendents of biologically distinct herders who migrated to South Africa at *ca.* 2000 BP (*cf.* Dreyer and Meiring 1937, 1952; A. B. Smith 1983, 1986, 1990, 1992; A. B. Smith *et al.* 1991; P. Smith *et al.* 1992; Yates and A. B. Smith 1993). Instead, differences in stature between hunter-gatherers and herders may be explained by two alternatives to gene flow, namely, (1) *in situ* genetic differentiation due to emerging social and economic differences between the practitioners of the two life ways; and (2) hunter-gatherers and herders having differential access to high nutrient resources.

Post-2000 BP Khoesan may have started to differentiate biologically into San and Khoekhoe populations due to growing *in situ* social and economic differences between herders and hunter-gatherers after some indigenous hunter-gatherers had acquired domestic stock from herders further north. This hypothesis was first suggested by Hausman (1980). As demonstrated in Chapter 7, crania from the post-2000 BP period display a minor, but significant increase in inter-individual distances in comparison to pre-2000 BP crania. As suggested by Elphick (1985) and Parkington and Hall (1987), the nature of hunting-and-gathering appeared to have changed during the last 2000 years due

to ecological and social pressures exerted on non-stock owners by those who owned stock. Parkington and Hall (1987) note further that herder groups appeared to have dominated the political, social and economic spheres during the last 2000 years. The social, economic and political separation between stock-owners and those lacking in stock may have grown stronger with time, eventually leading to the erection of social barriers to gene flow between hunter-gatherers and herders. This lack of gene flow between the two populations may eventually have expressed itself in morphological differentiation between the practitioners of the different life ways. The archaeological record is consistent with the gradual establishment of pastoralism in the region. As noted by Sadr (1998), traces of herders are often quite ephemeral between 2000 and 1000 BP and do not resemble the sophisticated cattle herding societies that European colonists described on their arrival at the Cape. The emergence of these cattle herding societies may have been a relatively recent development, possibly dating to the second millennium AD.

The results attained in this thesis are also consistent with the Khoesan remaining a single biological population after 2000 BP. Under this scenario, differences in body size and robusticity levels between hunter-gatherers and herders may be explained by differential access to high nutrient resources. Several researchers have suggested that hunter-gatherer and herder archaeological remains in the post-2000 BP period can probably be attributed to people from the same biological population moving back and forth between the two economic strategies (Marks 1972; Schrire 1980, 1992; Elphick 1985; Schrire and J. Deacon 1989). As mentioned above, herder groups appeared to have dominated the

political, social and economic spheres during the last 2000 years. Marginal groups, usually those without any stock or those who had lost stock, were consequently pushed to the periphery of society. At the same time, these groups were also forced out of the higher nutrient coastal forelands, towards the more marginal inland mountainous regions (Parkington and Hall 1987). Colonial era accounts often make mention of impoverished marginalised groups living in the mountainous regions of the Cape (Thom 1958). There, these populations usually survived by hunting-and-gathering and stock rustling (Elphick 1985). The nutritional and social stress that post-2000 BP hunter-gatherer groups would have been placed under, could explain why they may have been smaller than people who owned stock. In contrast, stock owners not only had access to higher nutrient regions, unlike hunter-gatherers, they also had access to a regular supply of milk, which could have aided growth during childhood, thus allowing them to reach their full growth potential (Hausman 1980).

POPULATION CONTINUITY IN THE SOUTH AFRICAN HOLOCENE

Many human populations around the world display temporal changes in craniofacial form at different times during the Holocene. Although this may be due to gene flow, gene flow is not always the cause. It is pertinent to heed the warnings of Swedlund and Anderson (2003) and Van Vark *et al.* (2003) regarding the likely cause of craniofacial change in the Americas. Although there now appears to be a consensus view emerging that craniofacial differences between early Holocene and late Holocene populations are the result of multiple human migrations (Neves *et al.* 1998; Neves and Pucciarelli 1998; Neves *et al.* 1999a, b; Owsley and Jantz 1999; J. F. Powell and Neves 1999; Jantz and Owsley 2001;

González-José *et al.* 2003, 2005; Neves *et al.* 2003; Neves and Hubbe 2005), Swedlund and Anderson (2003) and Van Vark *et al.* (2003) have cautioned that *in situ* biological change cannot be discounted. These authors argue that *in situ* genetic factors such as mutation, genetic drift and natural selection, as well as non-genetic factors such as environmental plasticity, may also account for the morphological changes seen in the Native American fossil record. Except for the migration of Negroid farmers into the eastern region during the last 2000 years, there is little biological evidence to support gene flow into the research region at any time during the last ten thousand years. Instead, cultural and subsistence changes at various stages during the Holocene are likely to be indicative of changing environmental and social pressures on indigenous populations. These changing pressures, rather than migrations, are likely to be behind the craniofacial changes evident in coastal LSA Khoesan populations.

The results achieved in this thesis also favour population continuity in coastal Khoesan populations during the Holocene, variation in craniofacial morphology notwithstanding. Small, but significant reductions in relative neurocranial dimensions during the Holocene appear to date to at least the early Holocene. In addition to the general reduction in neurocranial dimensions during the Holocene, there is a secondary fluctuation in overall craniofacial size at the end of the mid-Holocene/beginning late Holocene. Reductions in cranial size and accompanying allometric shape changes during this time are in all probability the result of environmental factors, and related to dietary and social stress due to an increase in population. The fact that there was a recovery in cranial size and a return to pre-5000 BP facial and frontal bone shape is indicative of developmental plasticity

rather than genetic factors. It was probably related to a general recovery in the dietary-related health status of indigenous populations after a decline between 4000 and 3000 BP. As such, it represents indigenous populations once more achieving their growth potential after having recovered from growth difficulties. This pattern of change would explain the observations of early researchers regarding morphological similarities between then seemingly unrelated crania of indigenous pre-4000 BP hunter-gatherer populations from the sites of Matjes River Rock Shelter and Oakhurst Cave, and the crania of supposed recent immigrant Khoekhoe (Drennan 1938; Rightmire 1970; Hausman 1980). Relatively large, robust cranial morphology such as that displayed by pre-5000 BP and post-2000 BP populations appears to have been the normal condition in the Khoesan for much of the Holocene, and not small, gracile crania as previously thought (Bräuer and Rösing 1989).

IMPLICATIONS OF THIS STUDY FOR UNDERSTANDING THE EMERGENCE OF RECENT PATTERNS OF HUMAN CRANIOFACIAL MORPHOLOGY

Apart from providing a biological perspective on human occupation along South Africa's western, south-western, southern and south-eastern coasts and coastal forelands during the Holocene, this study also contributes to an understanding of some of the probable processes involved in the emergence of recent patterns of human craniofacial morphology. In particular, this study demonstrates that what many previous researchers perceived as 'real' differences in cranial form, indicative of gene flow from other regions, can be explained by human plasticity under times of serious stress. It also demonstrates

that thinking about morphology in terms of individuals and variation through time paints a remarkably different picture from thinking about morphology in terms of population means.

An important issue which pervades studies focussed on the origins of recent patterns of human craniofacial variation, concerns the relative influence of genetic versus environmental factors on craniofacial form. This study has demonstrated that environmental processes, in this case dietary constraints, can influence craniofacial form. However, like some other recent studies have also demonstrated (Lahr and R. V. S. Wright 1996; Wood and Lieberman 2001; González-Jozé *et al.* 2005), the effects of environmental processes are limited and tend affect certain regions of the cranium more than others. This study confirms that the form of the viscerocranium is easily influenced by changes in environmental factors, while the neurocranium and basicranium is more stable. It also demonstrates that overall cranial size and levels of robusticity may change relatively quickly in response to changes in environmental factors. Because viscerocranial form and overall craniofacial size and robusticity are easily affected by environmental factors, these traits should be de-emphasised in studies investigating long term population continuity. Significantly, changes in craniofacial size and robusticity were often interpreted by early studies as evidence for population change in South Africa during the Holocene (Meiring 1937, 1953; Hoffman 1958; Louw 1960). The current study demonstrates that fluctuations in craniofacial size and robusticity, as well as accompanying allometric changes had little influence on the overall Khoesan cranial *bau plan* during the Holocene. This result is consistent with the observation by Relethford

(2004) that environmental plasticity may affect cranial form, but it does not appear to mask the effects that genes have on overall craniofacial morphology.

The current analysis also illustrates the value of analysing individual variation across time instead of using population means. Many previous studies which investigated morphological differences between San and Khoekhoe crania, pooled samples of recent San populations and pre-2000 BP archaeological samples in the belief that these two populations represented a single unchanged hunter-gatherer population. At the time, this assumption appeared justified since pre-2000 BP crania were generally small and gracile, like recent San hunter-gatherer crania. Significantly though, a large proportion of our sample of pre-2000 BP human remains appears to date between 4000 and 2000 BP, a time when Khoesan craniofacial size and robusticity was at its lowest. Even if some pre-5000 BP crania were included in the pre-2000 BP samples analysed by previous researchers, the dominance of small gracile crania in these samples would have served to drag down group means. It is thus unsurprising that small, gracile craniofacial morphology had been taken as typical of pre-2000 BP populations in previous analyses. It is only now that we have a larger sample of dated crania that we can see that small, gracile craniofacial morphology was not typical of the entire pre-2000 BP period.

FUTURE RESEARCH

The biological history of the Khoesan remains critically under-researched. The research carried out in this thesis has however laid the foundation for a number of follow-up projects. With an eye on future research, this project has increased the number of dated

archaeological Khoesan crania (some with associated post-cranial skeletons) in South African institutions by more than 100 specimens. The dates generated during the course of this project, together with other recent projects on the Khoesan, provide an invaluable resource for future studies. We are only now beginning to expose and understand prehistoric Khoesan biological evolution and further studies on larger dated samples are required to increase the resolution of morphological change.

A future project which could supplement the craniometric data from this project is an analysis of dental metric and non-metric traits. Whereas overall craniofacial form appears to be under genetic control, environmental plasticity does influence the form of certain regions of the cranium (e.g. viscerocranium), as demonstrated in this thesis. Like the neurocranium and basicranium, dental metric and non-metric traits appear to be less influenced by environmental factors (Wood and Lieberman 2001). An analysis of these traits may provide a further test of population continuity. Such a study could also include an analysis of cranial non-metric traits.

Another area in which we require further research is in the origins of Khoesan craniofacial morphology. Little work has been done in this area, as we have very few crania pre-dating 5000 BP and even fewer predating the Holocene. Yet understanding the terminal Pleistocene/early Holocene biological history of South African human populations is essential if we are to build a more complete picture of the emergence of Khoesan craniofacial morphology. Future projects on Khoesan craniofacial evolution should continue with the dating program started in this project in an effort to identify

more early cranial specimens. Since many of these early specimens are fragmentary, these projects should also develop ways to maximise data collection on crania regardless of preservation. This could include the collection of non-metric data on teeth and cranial fragments, along with the collection of metric data where possible. In addition to traditional data collection methods, newer methods based on computed tomography (CT) could also be used to *virtually* reconstruct missing parts in specimens.

CONCLUSION

This thesis investigated patterns of craniofacial variation in South African Khoesan populations during the last 12 000 years with the aim of establishing when and how recent patterns of cranial morphology first emerged. It also informs on the biological history of now extinct Cape coastal Khoesan populations. Research has shown that a large part of the craniofacial variation displayed by contemporary human populations around the world first emerged during the terminal Pleistocene/Holocene. While there have been numerous studies documenting terminal Pleistocene/Holocene craniofacial modernisation in diverse human populations such as Australian Aborigines, Native Americans, Europeans and Asians, there has been a dearth of studies focussing on recent craniofacial evolution of sub-Saharan African populations. Consequently, very little is known about the craniofacial antiquity of these populations. My study contributes to addressing a deficiency in the growing literature on the emergence of recent patterns of human craniofacial variation.

The investigation centred on three focus areas: (1) the antiquity of Khoesan craniofacial morphology; (2) late mid-Holocene reductions in Khoesan body size; and (3) the introduction of herding and late Holocene population continuity/discontinuity. The results of this thesis indicate that Khoesan craniofacial morphology predated the Holocene. Although there was a noticeable fluctuation in cranial size and concomitant change in certain aspects of craniofacial shape during the late mid-Holocene and a gradual reduction in relative neurocranial size over the course of the Holocene, craniofacial form always remained distinctly Khoesan-like. This study has also demonstrated that it is unlikely that an immigrant herder population had contributed in any significant way to the gene pool, and thus craniofacial morphology, of indigenous Khoesan populations during the last 2000 years. Although post-2000 BP crania display a minor increase in inter-individual distances compared to pre-2000 BP crania, this increase was not accompanied by any major change in craniofacial form at 2000 BP. Although the results of this study do not support a large scale migration of biologically distinct herders into the region at 2000 BP, they are not inconsistent with the possibility that *in situ* biological differences may have started to develop between hunter-gatherers and herders. Thus, unlike earlier claims that recent Khoesan populations may be the result of gene flow between indigenous and various immigrant populations, the current results suggest that there was population continuity in Holocene Khoesan populations in the research region. The results also indicate that relatively large, robust cranial morphology existed for much of the Holocene. Although the Khoesan are traditionally thought of as small and gracile in terms of cranial and post-cranial skeletal dimensions, this morphology was only dominant between 4000 and 3000 BP when nutritional insufficiencies due to an increase

in population appeared to have led to a widespread decrease in overall body dimensions. Significantly these changes did not obscure the typically Khoesan craniofacial morphological patterning in place since the terminal Pleistocene.

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APPENDICES

Appendix 1: The repeatability of the 190 linear measurements.

Measurements	Repeatability
B-1/2BN	0.990
B-N	0.996
B-NS	0.998
B-PR	0.999
B-D	0.996
B-ZYO	0.997
B-FMO	0.997
B-ZYM	0.998
B-PTP	0.994
B-P	0.998
B-1/2BL	0.995
B-AST	0.998
B-L	0.998
B-O	0.998
B-BA	0.999
B-BOC	0.997
B-H	0.998
B-TSP	0.998
B-MXT	0.997
1/2BN-N	0.988
1/2BN-NS	0.998
1/2BN-PR	0.973
1/2BN-D	0.992
1/2BNZYO	0.993
1/2BN-FMO	0.997
1/2BN-ZYM	0.999
1/2BN-PTP	0.998
1/2BN-P	0.997
1/2BN-1/2BL	0.998
1/2BN-AST	0.998
172BN-L	0.999
1/2BN-0	0.999
1/2BN-BA	0.999
1/2BN-BOC	0.998
1/2BN-H	0.997
1/2BN-TSP	0.997
1/2BN-MXT	0.997
N-NS	0.997
N-PR	0.996
N-D	0.977
N-ZYO	0.971
N-FMO	0.989
N-ZYM	0.996

Table continued:

N-PTP	0.999
N-P	0.993
N-1/2BL	0.998
N-AST	0.997
N-L	0.996
N-O	0.999
N-BA	0.997
N-BOC	0.992
N-H	0.993
N-TSP	0.988
N-MXT	0.995
NS-PR	0.996
NS-D	0.992
NS-ZYO	0.981
NS-FMO	0.997
NS-ZYM	0.993
NS-PTP	0.999
NS-P	0.992
NS-1/2BL	0.998
NS-AST	0.993
NS-L	0.996
NS-O	0.994
NS-BA	0.989
NS-BOC	0.974
NS-H	0.984
NS-TSP	0.983
NS-MXT	0.982
PR-D	0.994
PR-ZYO	0.983
PR-FMO	0.998
PR-ZYM	0.993
PR-PTP	0.999
PR-P	0.994
PR-1/2BL	0.999
PR-AST	0.995
PR-L	0.999
PR-O	0.998
PR-BA	0.993
PR-BOC	0.985
PR-H	0.991
PR-TSP	0.987
PR-MXT	0.991
D-ZYO	0.942
D-FMO	0.987
D-ZYM	0.994
D-PTP	0.998
D-P	0.986

Table continued:

D-1/2BL	0.998
D-AST	0.995
D-L	0.998
D-O	0.997
D-BA	0.993
D-BOC	0.982
D-H	0.982
D-TSP	0.981
D-MXT	0.986
ZYO-FMO	0.954
ZYO-ZYM	0.988
ZYO-PTP	0.998
ZYO-P	0.977
ZYO-1/2BL	0.997
ZYO-AST	0.994
ZYO-L	0.998
ZYO-O	0.997
ZYO-BA	0.995
ZYO-BOC	0.983
ZYO-H	0.988
ZYO-TSP	0.975
ZYO-MXT	0.99
FMO-ZYM	0.998
FMO-PTP	0.999
FMO-P	0.992
FMO-1/2BL	0.999
FMO-AST	0.995
FMO-L	0.999
FMO-O	0.998
FMO-BA	0.997
FMO-BOC	0.995
FMO-H	0.995
FMO-TSP	0.985
FMO-MXT	0.993
ZYM-PTP	0.998
ZYM-P	0.981
ZYM-1/2BL	0.998
ZYM-AST	0.994
ZYM-L	0.998
ZYM-O	0.997
ZYM-BA	0.992
ZYM-BOC	0.992
ZYM-H	0.991
ZYM-TSP	0.98
ZYM-MXT	0.971
PTP-P	0.994
PTP-1/2BL	0.998

Table continued:

PTP-AST	0.991
PTP-L	0.998
PTP-O	0.998
PTP-BA	0.998
PTP-BOC	0.998
PTP-H	0.998
PTP-TSP	0.997
PTP-MXT	0.997
P-1/2BA	0.998
P-AST	0.985
P-L	0.996
P-O	0.994
P-BA	0.992
P-BOC	0.99
P-H	0.992
P-TSP	0.982
P-MXT	0.988
½BL-AST	0.995
½BL-L	0.994
½BL-O	0.998
½BL-BA	0.998
½BL-BOC	0.994
½BL-H	0.998
½BL-TSP	0.996
½BL-MXT	0.997
AST-L	0.99
AST-0	0.984
AST-BA	0.992
AST-BOC	0.992
AST-H	0.996
AST-TSP	0.988
AST-MXT	0.993
L-O	0.998
L-BA	0.996
L-BOC	0.996
L-H	0.997
L-TSP	0.99
L-MXT	0.997
O-BA	0.99
O-BOC	0.996
O-H	0.995
O-TSP	0.978
O-MXT	0.994
BA-BOC	0.989
BA-H	0.99
BA-TSP	0.968
BA-MXT	0.985

Table continued:

BOC-H	0.976
BOC-TSP	0.98
BOC-MXT	0.985
H-TSP	0.989
H-MXT	0.989
TSP-MXT	0.984

Appendix 2: The repeatability of the 20 cranial landmarks used in this thesis.

Landmarks	Repeatability
B	0.998
1/2BN	0.998
N	0.994
NS	0.987
PR	0.995
D	0.998
ZYO	0.977
FMO	0.991
ZYM	0.989
PTP	0.998
P	0.99
1/2BL	0.997
AST	0.989
L	0.997
O	0.995
BA	0.995
BOC	0.99
H	0.99
TSP	0.994
MXT	0.988

Appendix 3: Mahalanobis distances (D) between all male crania.

		UCT262	NMB1207	UCT583	UCT157	SAM4867	SAM6020	SAM5035a	NMB1219	NMB1338	UCT114	UCT83	SAM1446	SAM5032
		510±40	560±50	560±45	587±28	590±45	620±30	620±35	650±60	650±35	650±40	680±40	740±30	765±25
UCT262	510±40	0												
NMB1207	560±50	8.01	0											
UCT583	560±45	9.12	8.74	0										
UCT157	587±28	9.20	10.02	9.42	0									
SAM4867	590±45	8.97	10.01	8.44	8.75	0								
SAM6020	620±30	8.54	8.58	8.21	7.93	9.58	0							
SAM5035a	620±35	9.91	9.84	9.51	8.68	9.62	9.52	0						
NMB1219	650±60	9.59	10.04	8.57	9.72	8.89	9.41	10.05	0					
NMB1338	650±35	9.80	8.13	9.57	9.85	9.89	8.34	10.41	10.21	0				
UCT114	650±40	9.24	9.45	9.03	10.44	8.13	10.05	8.91	9.42	9.94	0			
UCT83	680±40	9.91	9.21	9.11	9.79	8.36	9.45	10.31	10.18	9.87	9.23	0		
SAM1446	740±30	9.36	9.28	8.15	9.58	9.27	7.90	10.61	10.42	9.36	8.63	9.26	0	
SAM5032	765±25	10.10	9.68	8.86	9.49	9.31	9.21	10.57	9.72	9.90	9.94	10.41	9.88	0
A2226	800±50	10.36	11.29	9.84	9.65	10.22	9.51	10.99	**11.77**	10.11	10.25	**11.45**	9.89	10.43
A1154	905±25	8.33	9.11	9.16	9.06	10.26	7.97	10.99	9.76	10.07	10.37	10.38	9.22	10.00
UCT70	920±40	10.08	9.40	8.63	8.51	7.95	8.97	8.94	9.59	8.76	9.04	9.79	9.03	9.43
UCT60	950±50	8.46	9.50	7.90	9.53	8.09	8.72	9.18	9.21	8.53	10.01	9.14	9.21	8.54
SAM6332	980±50	9.91	9.55	8.72	10.27	8.57	9.58	9.17	9.69	9.39	9.46	9.34	7.98	9.64
UCT227	1000±50	8.46	8.43	7.90	8.51	9.69	8.92	8.01	8.74	8.35	8.83	9.65	8.72	9.11
SAM1260	1137±27	11.03	11.03	9.76	11.08	10.14	10.71	11.90	**11.42**	9.91	10.75	**12.54**	10.16	**11.68**
A2227	1150±50	**12.60**	**12.93**	10.86	**11.48**	**12.15**	**11.57**	**12.07**	**12.15**	10.76	**11.51**	**12.13**	10.72	**12.34**
SAM4905	1210±50	10.13	9.65	9.17	8.34	9.67	8.44	9.99	9.57	10.27	10.18	10.55	9.72	9.76
SAM4898	1226±26	9.30	8.54	7.58	8.72	9.16	7.84	9.75	9.58	8.36	9.99	10.82	9.69	10.84
SAM6074	1360±40	8.99	8.76	9.03	9.10	8.73	9.72	9.59	10.08	9.35	9.69	9.42	10.06	10.00
NMB1707	1394±24	10.53	8.78	8.40	10.13	10.28	9.86	10.89	10.69	9.46	10.31	10.05	10.02	9.09
SAM6334	1400±50	9.62	10.16	9.11	9.15	9.97	8.53	10.77	10.50	9.91	10.48	10.22	10.30	8.92
SAM4874	1426±29	8.15	7.87	8.09	9.18	7.75	7.30	8.37	8.64	7.39	8.29	9.32	8.45	8.38
SAM6149	1440±70	8.65	9.70	8.57	9.94	9.61	8.95	9.90	10.49	10.19	9.40	11.22	9.33	9.72
SAM5083	1490±50	8.86	10.14	7.88	8.83	8.43	7.55	8.67	9.21	9.46	9.46	9.83	9.30	8.93
SAM6213	1558±27	11.10	9.84	8.88	9.97	10.18	9.56	10.88	10.42	10.29	9.36	10.10	10.56	10.95
UCT109	1590±50	9.41	9.72	9.91	7.89	8.98	7.73	8.94	9.38	9.73	9.85	9.20	9.04	9.16
NMB83	1590±40	10.31	10.03	10.34	9.86	10.50	9.44	10.36	9.10	9.75	8.80	**11.90**	11.37	9.76
SAM320g	1707±27	9.41	10.15	9.57	10.68	8.83	10.73	10.79	11.38	11.11	9.13	10.74	10.62	10.13

SAM4630	1775±80	10.47	10.91	9.84	11.32	10.66	10.85	11.21	10.54	10.85	10.19	10.77	11.16	**11.64**
A1166	1818±27	8.48	9.85	10.26	11.20	10.94	9.58	11.66	11.15	10.09	10.79	**11.93**	8.82	**11.88**
SAM6041a	1824±27	9.96	10.24	9.96	10.47	9.69	9.03	9.90	11.00	9.85	9.25	9.57	9.65	10.02
A1152	1850±35	11.07	10.87	10.27	10.01	9.95	10.85	11.19	11.05	11.00	9.85	10.77	9.78	11.27
UCT429	1870±35	9.87	9.38	10.27	10.95	10.08	9.87	9.90	11.10	10.89	9.64	10.83	11.00	10.83
SAM1473	1880±60	8.39	8.95	9.28	9.85	7.86	8.84	9.60	9.64	9.07	8.47	10.51	9.47	9.14
SAM4901	1892±28	10.36	10.74	9.24	8.59	8.92	9.05	9.82	9.50	8.64	9.65	9.79	9.51	10.47
SAM6264	1950±60	8.70	7.48	7.89	8.32	9.31	7.33	8.25	10.05	8.61	9.17	9.47	9.43	9.44
SAM3053	1990±50	10.76	9.25	9.81	9.73	10.00	9.17	9.26	8.94	8.98	10.27	9.69	10.34	9.79
SAM5035b	2011±30	10.70	9.55	10.05	8.87	8.72	9.92	10.37	9.78	10.28	11.03	10.85	11.35	10.56
SAM1443	2050±50	9.04	9.31	8.65	10.24	9.83	8.77	10.21	10.13	8.00	10.07	10.24	10.37	10.15
UCT387	2055±40	8.53	9.04	8.35	9.10	8.99	9.79	10.36	9.48	10.94	10.13	10.45	9.71	9.19
SAM1142	2090±27	10.06	9.60	8.96	9.27	8.98	9.36	9.42	8.71	9.49	8.95	9.70	9.18	9.93
UCT220	2100±21	9.50	9.63	8.67	9.77	9.59	9.52	8.91	9.22	9.68	8.77	9.71	9.96	9.46
SAM4636	2130±45	9.75	10.04	8.46	9.18	9.30	9.25	10.00	10.23	9.28	9.16	10.73	9.73	9.50
SAM6313b	2140±29	9.27	10.00	8.20	8.78	8.29	7.89	9.68	9.93	9.17	9.11	9.35	8.54	9.93
SAM5082	2150±60	8.72	8.95	8.55	8.52	8.58	8.24	9.57	9.75	9.96	9.49	10.10	10.26	8.18
SAM1441	2170±60	8.96	9.54	8.57	8.70	9.48	9.87	9.17	10.22	10.10	9.61	10.32	9.16	9.88
UCT134	2210±40	9.83	10.35	8.99	10.27	8.92	10.09	10.29	9.29	10.87	10.03	10.51	**11.43**	9.83
SAM4942	2220±45	8.63	9.57	9.07	9.16	8.49	9.36	10.73	9.31	9.74	8.24	9.76	9.24	10.17
A1114	2271±33	9.96	10.68	10.57	9.81	9.86	10.02	10.27	10.54	9.92	10.53	9.70	10.31	**11.81**
UCT107	2290±50	9.29	9.30	10.18	9.59	9.46	8.54	10.35	9.73	8.77	9.15	10.60	9.51	9.64
SAM6043	2295±28	9.44	10.57	9.24	10.92	9.59	9.21	9.64	10.59	9.76	9.63	9.25	9.18	10.33
SAM34	2310±25	9.53	9.89	10.03	9.16	9.30	8.40	9.81	9.75	8.07	9.51	10.15	9.64	9.87
SAM1146	2321±28	9.56	9.26	9.54	8.57	8.87	8.98	9.83	11.10	9.59	9.69	9.31	9.28	10.59
NMB82	2335±40	9.66	8.39	9.57	9.68	9.18	8.54	10.18	9.24	9.40	8.59	10.44	8.91	9.74
SAM4899	2440±60	9.09	8.55	8.23	9.55	9.61	7.56	8.55	8.81	9.03	9.17	10.13	8.07	10.21
ALB222	2540±60	9.55	9.04	9.36	9.16	9.11	9.53	10.51	9.65	10.09	9.69	9.80	8.76	10.31
ALB301	2570±50	9.86	8.94	9.82	10.30	10.05	10.30	10.27	9.49	10.93	9.35	10.47	11.26	9.79
A1115	2588±28	9.52	10.99	9.84	9.47	9.66	9.83	10.77	11.12	10.13	10.70	10.70	10.69	10.95
UCT167	2695±45	8.07	8.23	8.69	8.71	9.03	7.44	8.82	9.77	8.57	8.67	9.33	8.52	9.51
UCT445	2720±60	9.70	10.13	9.44	9.68	10.70	10.58	11.31	10.12	10.49	10.06	10.70	10.33	10.96
SAM5049	2740±50	9.23	8.15	9.15	10.10	8.84	8.63	9.80	9.98	9.36	9.19	10.13	9.04	8.67
SAM5048	2780±60	10.37	9.99	9.22	9.84	10.33	9.10	9.71	10.96	10.39	8.72	10.67	9.89	8.94
UCT162	2880±50	9.61	9.67	8.70	10.05	9.44	9.12	10.60	10.40	10.83	9.44	10.10	9.71	9.74
SAM6147	2920±60	8.61	9.27	9.81	8.09	9.20	9.48	8.58	9.41	9.82	9.47	9.37	10.03	9.67
SAM6071	2935±32	8.78	9.22	8.73	8.48	9.60	8.15	9.33	9.50	9.31	9.54	8.24	9.48	9.79
SAM6317	2970±60	9.54	9.94	8.52	9.87	9.62	8.69	10.41	9.96	9.67	9.94	10.49	8.90	8.74

NMB1242	3030±26	8.29	9.97	9.23	8.77	9.24	9.41	9.83	9.21	9.88	9.87	10.63	9.44	9.64
NMB1273	3050±60	8.42	8.36	7.93	9.22	9.44	8.58	9.30	9.58	9.68	8.21	9.68	9.04	9.75
NMB1202	3140±50	9.38	8.82	8.02	9.27	9.51	8.82	9.42	8.48	9.59	9.26	9.52	9.58	9.09
SAM1145	3210±70	9.37	8.94	9.02	10.43	9.64	8.22	10.00	10.27	8.95	9.25	9.85	9.32	9.77
NMB4	3236±33	9.49	9.65	9.52	10.73	10.06	9.06	10.28	10.85	10.52	9.58	11.74	9.92	**11.81**
SAM6318	3310±60	7.71	8.77	9.58	8.47	9.60	8.78	8.41	10.22	9.78	9.35	9.57	9.78	10.07
SAM1879	3440±60	9.30	9.49	8.75	8.58	9.61	8.25	8.46	9.49	8.94	9.25	10.41	9.52	9.02
SAM31	3576±30	**11.89**	11.04	9.72	10.87	9.98	9.54	10.86	10.85	10.75	10.50	9.91	10.99	10.99
SAM4931	3750±60	9.46	10.19	8.78	9.57	10.24	8.81	11.23	9.73	9.54	9.44	10.45	9.43	9.80
SAM32	3754±35	9.18	8.78	7.61	9.53	10.34	9.51	9.45	10.01	9.15	10.34	10.66	8.86	10.56
A1124	4320±32	11.04	10.65	10.97	10.52	10.02	10.39	**11.64**	10.46	10.03	10.73	**11.91**	10.55	10.59
UCT112	4445±50	9.27	10.68	9.20	10.52	10.10	9.06	9.82	10.05	10.04	9.73	10.61	10.74	10.28
ALB131	4700±60	8.68	7.50	8.72	8.96	8.52	8.93	8.89	8.20	9.73	7.77	8.88	8.23	9.75
NMB1275	4850±60	7.85	7.94	7.87	8.70	8.27	7.38	9.36	9.55	8.12	8.58	8.54	8.14	9.42
SAM6272	5830±80	9.29	10.08	7.95	9.67	9.24	9.08	10.33	9.30	10.01	9.66	10.43	9.38	9.17
UCT180	6180±70	9.09	9.52	8.96	9.67	10.27	9.19	11.15	10.10	9.79	10.42	10.39	9.47	9.97
SAM4182	6811±36	9.80	9.69	9.25	10.25	9.24	10.10	10.05	11.07	8.50	9.97	9.52	9.73	10.51
SAM5055	6995±50	9.96	10.13	9.92	10.41	9.44	10.20	10.24	10.24	9.54	10.04	10.67	10.52	11.16
UCT156	10110±80	10.27	9.92	10.07	9.36	10.06	9.75	9.26	9.96	10.05	9.75	10.54	10.73	10.93
SAM4692	*ca.*12000	10.10	10.08	10.55	10.36	10.79	10.36	11.05	10.50	9.32	9.32	10.68	10.53	9.19

Table continued:

		A2226 800±50	A1154 905±25	UCT70 920±40	UCT60 950±50	SAM6332 980±50	UCT227 1000±50	SAM1260 1137±27	A2227 1150±50	SAM4905 1210±50	SAM4898 1226±26	SAM6074 1360±40	NMB1707 1394±24	SAM6334 1400±50
UCT262	510±40													
NMB1207	560±50													
UCT583	560±45													
UCT157	587±28													
SAM4867	590±45													
SAM6020	620±30													
SAM5035a	620±35													
NMB1219	650±60													
NMB1338	650±35													
UCT114	650±40													
UCT83	680±40													
SAM1446	740±30													
SAM5032	765±25													
A2226	800±50	0												
A1154	905±25	10.29	0											
UCT70	920±40	9.20	9.81	0										
UCT60	950±50	9.19	9.57	8.98	0									
SAM6332	980±50	11.03	9.36	8.24	8.72	0								
UCT227	1000±50	9.77	9.32	7.96	8.00	8.26	0							
SAM1260	1137±27	**11.76**	10.96	10.12	10.53	10.06	9.96	0						
A2227	1150±50	10.95	**11.63**	10.74	11.24	11.20	**11.50**	**12.43**	0					
SAM4905	1210±50	10.35	9.36	8.77	9.67	9.66	9.43	10.23	11.25	0				
SAM4898	1226±26	8.68	9.56	7.91	8.56	9.73	7.92	11.05	11.07	9.68	0			
SAM6074	1360±40	**11.41**	9.67	9.53	8.65	8.28	9.34	10.57	**12.36**	9.74	8.92	0		
NMB1707	1394±24	10.43	10.51	10.36	8.82	10.85	9.10	11.38	**11.54**	11.03	8.99	9.76	0	
SAM6334	1400±50	11.39	9.10	9.75	9.38	10.28	9.19	10.28	11.19	10.06	9.85	8.81	9.61	0
SAM4874	1426±29	9.42	8.46	7.45	7.75	7.60	8.18	10.40	**11.84**	8.88	8.43	8.35	10.12	9.23
SAM6149	1440±70	8.70	8.98	9.24	9.46	9.01	9.42	10.54	**11.86**	10.10	8.96	9.11	10.07	10.04
SAM5083	1490±50	10.55	8.54	8.62	9.06	8.29	7.98	10.14	10.57	8.97	8.79	9.75	9.18	8.96
SAM6213	1558±27	10.80	9.34	9.11	9.16	10.72	10.04	10.75	**12.07**	9.52	9.44	9.32	10.03	10.40
UCT109	1590±50	8.77	9.73	8.38	8.37	9.04	8.18	10.91	**12.12**	9.19	9.40	10.13	10.00	10.32
NMB83	1590±40	10.91	10.32	9.99	10.95	10.65	10.66	**11.42**	**12.14**	9.48	10.43	10.83	11.22	11.08
SAM320g	1707±27	10.97	10.57	8.81	10.12	8.87	9.38	10.38	**12.55**	9.26	9.94	9.61	10.58	10.79
SAM4630	1775±80	**11.41**	10.40	10.59	9.48	9.71	9.83	**12.15**	**13.56**	**12.56**	9.64	10.30	11.36	**12.28**
A1166	1818±27	**12.22**	9.57	9.37	10.44	9.21	10.43	10.91	**11.99**	10.44	10.55	10.10	**12.01**	**11.48**

SAM6041a	1824±27	9.87	9.52	8.99	9.00	9.62	9.91	10.39	**11.45**	10.18	10.87	9.90	10.60	9.96
A1152	1850±35	11.02	9.84	8.49	10.95	9.72	10.87	**12.16**	10.16	10.74	10.77	10.31	**11.51**	11.05
UCT429	1870±35	10.59	10.27	9.33	10.78	10.84	10.61	**12.17**	**12.00**	10.39	10.48	**11.74**	10.23	10.78
SAM1473	1880±60	10.21	10.11	9.15	8.67	9.49	9.38	11.03	**11.47**	8.96	8.61	9.77	11.08	10.26
SAM4901	1892±28	11.04	10.46	8.17	9.21	9.71	8.76	11.11	**11.52**	10.05	8.74	9.46	10.71	10.07
SAM6264	1950±60	9.77	9.03	8.04	8.25	8.71	8.55	10.32	**11.91**	8.71	8.28	8.64	9.21	8.96
SAM3053	1990±50	**11.97**	10.16	9.46	8.81	9.06	8.30	11.07	**12.56**	9.96	10.15	9.50	10.73	10.78
SAM5035b	2011±30	10.08	10.58	9.98	9.92	10.28	9.86	10.09	**12.43**	9.63	9.58	10.49	10.54	10.39
SAM1443	2050±50	10.59	**11.41**	10.11	8.43	10.28	10.17	**11.49**	11.06	9.38	9.35	9.21	10.63	10.99
UCT387	2055±40	10.34	9.14	8.45	7.65	10.08	9.13	11.15	**12.29**	8.78	9.41	9.10	10.20	9.53
SAM1142	2090±27	10.87	9.95	9.36	8.42	9.45	9.51	10.10	10.71	9.48	9.30	8.68	9.71	8.73
UCT220	2100±21	10.73	9.81	9.51	9.68	9.33	8.42	10.32	11.37	9.64	9.82	8.73	10.59	9.32
SAM4636	2130±45	10.14	8.83	8.09	8.58	9.15	8.71	9.59	**11.67**	9.18	9.42	9.17	10.72	8.82
SAM6313b	2140±29	8.90	9.12	9.67	8.26	9.80	9.53	11.00	11.12	9.12	7.86	9.26	9.07	9.04
SAM5082	2150±60	10.11	9.49	10.64	8.39	9.49	8.53	11.27	**13.06**	9.37	9.05	8.74	9.56	9.44
SAM1441	2170±60	10.51	9.59	8.58	9.20	8.82	8.09	9.51	10.94	8.87	9.79	10.24	10.72	9.98
UCT134	2210±40	**11.46**	10.28	10.29	9.43	10.33	8.81	**11.79**	**12.86**	9.88	10.29	10.21	11.13	9.98
SAM4942	2220±45	11.18	9.55	9.52	9.74	9.67	9.11	9.84	**12.52**	9.66	10.25	9.42	**11.42**	9.30
A1114	2271±33	10.99	10.44	9.92	10.06	9.08	10.85	10.96	10.67	10.72	10.80	9.80	10.11	11.31
UCT107	2290±50	10.63	9.17	9.12	8.77	10.19	8.66	10.08	**13.39**	8.52	9.41	9.72	9.78	8.99
SAM6043	2295±28	10.06	9.46	10.50	7.33	9.27	8.87	**11.58**	10.32	10.28	10.58	10.52	11.20	10.20
SAM34	2310±25	9.54	9.81	8.51	8.60	7.87	7.90	11.05	**12.09**	9.78	9.00	9.09	11.12	9.83
SAM1146	2321±28	10.06	9.82	7.15	8.46	8.71	9.20	10.50	**11.47**	8.84	9.03	9.79	9.76	10.11
NMB82	2335±40	9.90	8.62	8.60	9.53	8.29	9.34	10.15	10.49	9.59	8.45	9.30	10.87	9.55
SAM4899	2440±60	10.25	8.27	8.50	8.86	8.70	7.93	10.65	11.07	9.13	8.73	9.83	9.42	8.60
ALB222	2540±60	11.10	9.08	9.42	9.16	8.59	8.84	10.43	10.74	8.92	9.70	9.51	10.29	10.51
ALB301	2570±50	10.87	9.36	8.58	9.75	10.01	9.35	**12.42**	**11.97**	10.74	9.03	9.47	10.53	9.37
A1115	2588±28	9.51	8.81	9.41	10.39	9.96	9.67	**11.50**	11.31	10.19	10.02	10.01	10.99	10.81
UCT167	2695±45	9.94	9.05	8.90	8.68	8.09	8.41	10.73	**11.80**	9.17	9.14	8.81	10.42	9.15
UCT445	2720±60	**11.41**	9.88	10.46	10.01	9.46	9.25	10.76	**12.56**	10.56	10.10	10.22	10.56	11.00
SAM5049	2740±50	9.57	8.53	8.41	8.25	8.35	8.20	10.32	**12.49**	9.05	8.14	8.64	9.86	9.45
SAM5048	2780±60	10.17	10.84	10.25	9.90	9.17	9.03	10.51	**11.68**	8.67	9.94	9.75	9.41	10.15
UCT162	2880±50	10.74	10.04	8.94	9.69	10.19	9.03	11.00	**12.54**	10.30	9.93	10.12	10.51	10.39
SAM6147	2920±60	10.58	9.58	9.50	8.37	9.37	8.80	11.33	**12.76**	8.95	9.83	9.26	9.73	10.26
SAM6071	2935±32	10.97	8.94	8.99	8.90	9.29	8.08	10.89	10.91	9.32	8.97	9.28	10.59	8.27
SAM6317	2970±60	9.97	9.67	7.91	8.83	8.91	9.64	11.29	11.12	9.73	9.99	10.61	10.61	10.67
NMB1242	3030±26	8.99	8.55	9.72	8.76	8.58	8.76	10.44	**12.54**	9.00	9.59	9.57	9.84	10.14
NMB1273	3050±60	10.70	9.67	10.00	8.08	9.37	8.61	10.40	**11.75**	8.30	9.38	8.09	8.58	8.81

NMB1202	3140±50	10.20	9.20	9.04	8.35	8.88	7.89	10.64	**12.54**	9.06	8.88	9.45	9.38	10.19
SAM1145	3210±70	10.36	9.32	9.71	7.48	9.15	9.45	10.86	11.26	9.37	9.17	10.06	8.97	10.54
NMB4	3236±33	**11.91**	10.57	10.50	10.57	10.38	9.36	**11.53**	**12.83**	**11.77**	9.60	10.57	9.90	10.50
SAM6318	3310±60	9.98	9.78	8.55	8.73	8.77	8.85	**11.52**	10.11	8.95	8.95	9.46	10.12	9.31
SAM1879	3440±60	8.75	7.67	8.25	7.13	7.97	7.91	10.73	10.45	8.03	8.22	9.67	9.95	9.37
SAM31	3576±30	11.38	10.42	9.78	10.17	10.37	10.85	**12.06**	**12.82**	9.80	10.16	10.09	9.96	**11.52**
SAM4931	3750±60	9.46	8.89	9.46	9.10	9.42	7.71	10.80	11.23	9.16	8.68	9.68	10.29	9.27
SAM32	3754±35	10.62	9.44	9.24	9.15	8.95	7.83	11.09	9.62	7.83	8.82	9.71	10.67	10.50
A1124	4320±32	**12.92**	9.87	10.34	10.65	10.43	10.53	**12.29**	**11.98**	11.09	10.66	11.13	10.46	10.63
UCT112	4445±50	10.66	9.45	10.12	8.38	10.03	9.28	10.60	11.34	9.33	9.46	8.87	10.17	9.30
ALB131	4700±60	10.67	9.04	8.66	9.23	9.32	8.09	10.91	**13.01**	8.70	9.97	9.04	9.21	10.27
NMB1275	4850±60	10.32	8.96	8.55	9.10	8.34	8.07	10.44	**11.49**	9.79	8.14	8.55	9.79	9.09
SAM6272	5830±80	10.03	9.44	9.63	9.12	9.75	9.80	10.21	**11.45**	10.91	9.72	10.65	10.30	8.93
UCT180	6180±70	11.32	10.44	9.71	9.99	9.79	9.72	10.75	**12.01**	11.00	9.81	10.40	9.54	9.57
SAM4182	6811±36	10.12	10.40	10.00	8.71	9.65	9.39	10.87	**11.84**	10.62	9.20	9.12	10.37	10.25
SAM5055	6995±50	9.96	10.77	9.03	8.51	9.37	8.06	10.62	**13.40**	10.43	9.93	10.77	10.83	10.41
UCT156	10110±80	10.30	9.60	9.96	10.21	10.57	9.68	10.66	**12.18**	10.66	10.31	9.13	11.16	10.73
SAM4692	*ca.*12000	10.17	9.43	10.15	9.99	9.69	8.24	**11.75**	10.43	11.05	10.44	10.30	9.71	9.04

Table continued:

		SAM4874 1426±29	SAM6149 1440±70	SAM5083 1490±50	SAM6213 1558±27	UCT109 1590±50	NMB83 1590±40	SAM320g 1707±27	SAM4630 1775±80	A1166 1818±27	SAM6041a 1824±27	A1152 1850±35	UCT429 1870±35	SAM1473 1880±60
UCT262	510±40													
NMB1207	560±50													
UCT583	560±45													
UCT157	587±28													
SAM4867	590±45													
SAM6020	620±30													
SAM5035a	620±35													
NMB1219	650±60													
NMB1338	650±35													
UCT114	650±40													
UCT83	680±40													
SAM1446	740±30													
SAM5032	765±25													
A2226	800±50													
A1154	905±25													
UCT70	920±40													
UCT60	950±50													
SAM6332	980±50													
UCT227	1000±50													
SAM1260	1137±27													
A2227	1150±50													
SAM4905	1210±50													
SAM4898	1226±26													
SAM6074	1360±40													
NMB1707	1394±24													
SAM6334	1400±50													
SAM4874	1426±29	0												
SAM6149	1440±70	8.65	0											
SAM5083	1490±50	8.44	10.02	0										
SAM6213	1558±27	9.55	9.16	10.36	0									
UCT109	1590±50	8.86	10.12	8.23	10.98	0								
NMB83	1590±40	8.83	9.29	10.49	9.86	10.70	0							
SAM320g	1707±27	8.63	10.48	9.64	10.91	9.61	10.97	0						
SAM4630	1775±80	9.86	11.32	10.55	10.74	10.30	11.02	10.87	0					
A1166	1818±27	8.29	11.28	9.60	**11.86**	11.04	10.92	9.81	**11.52**	0				

SAM6041a	1824±27	8.08	10.83	8.14	10.12	8.97	11.02	10.10	10.56	10.15	0			
A1152	1850±35	10.54	11.16	10.52	10.17	11.16	10.64	**11.48**	**11.62**	10.70	10.88	0		
UCT429	1870±35	9.70	11.08	9.08	10.62	10.39	10.70	10.57	**11.67**	**11.65**	9.91	10.62	0	
SAM1473	1880±60	8.95	10.41	8.61	10.56	9.61	9.90	9.83	**11.44**	10.68	10.08	10.36	9.05	0
SAM4901	1892±28	8.68	10.60	9.17	9.36	9.91	10.33	10.86	11.34	11.10	10.49	10.59	11.26	8.78
SAM6264	1950±60	7.04	9.46	8.01	9.20	8.46	8.52	9.61	9.94	8.48	7.92	10.74	10.03	9.20
SAM3053	1990±50	8.54	10.93	10.15	10.73	8.93	9.92	10.32	11.34	11.30	9.79	**12.07**	**11.43**	10.72
SAM5035b	2011±30	8.83	10.44	9.89	10.67	9.70	**11.80**	10.82	**11.67**	**13.26**	10.62	**12.43**	10.02	10.86
SAM1443	2050±50	8.63	10.79	9.33	10.72	10.43	10.72	11.08	11.24	10.28	9.02	10.75	11.11	9.15
UCT387	2055±40	8.74	10.29	9.75	8.96	10.30	10.56	9.77	11.11	10.23	9.05	10.08	10.53	8.85
SAM1142	2090±27	8.83	10.03	9.31	8.63	9.91	8.73	10.45	10.18	10.06	9.55	9.44	9.69	9.85
UCT220	2100±21	9.20	9.79	8.77	10.05	10.64	9.67	10.63	10.80	11.20	10.09	10.05	10.40	8.80
SAM4636	2130±45	8.07	10.71	9.29	10.09	9.88	10.40	9.59	11.03	10.43	8.93	10.27	9.49	9.63
SAM6313b	2140±29	7.86	9.18	9.22	10.12	9.61	10.08	9.95	10.75	**11.47**	9.98	10.63	10.25	8.91
SAM5082	2150±60	8.47	9.98	8.69	10.14	8.90	9.54	8.62	10.43	11.33	10.43	**12.38**	9.72	8.32
SAM1441	2170±60	8.92	10.08	8.96	10.56	10.01	9.59	9.32	10.63	9.39	9.20	10.82	10.81	9.18
UCT134	2210±40	9.44	11.27	9.44	11.27	10.49	10.84	10.08	10.31	**12.69**	11.27	10.80	9.85	9.74
SAM4942	2220±45	8.48	9.92	9.96	10.76	9.95	9.80	10.67	11.04	10.60	10.21	11.16	10.32	9.28
A1114	2271±33	10.37	10.30	9.92	11.27	10.33	10.73	10.10	11.34	10.20	9.87	9.28	10.39	11.08
UCT107	2290±50	8.06	11.21	9.15	10.56	8.74	10.00	9.77	10.44	9.85	9.48	10.52	9.55	9.14
SAM6043	2295±28	8.80	10.61	9.28	10.33	9.97	11.02	11.39	**11.90**	10.73	10.15	10.49	10.99	9.11
SAM34	2310±25	7.08	9.68	9.18	9.85	9.63	10.34	9.82	10.05	10.21	10.17	10.54	10.83	9.63
SAM1146	2321±28	8.94	9.97	9.94	9.04	9.12	10.88	8.62	11.11	9.69	10.64	8.11	10.04	9.51
NMB82	2335±40	8.28	9.43	9.33	10.32	9.94	9.70	10.77	11.27	10.02	9.76	9.83	10.33	8.02
SAM4899	2440±60	7.39	9.86	9.17	10.22	10.15	9.86	9.93	10.57	9.44	9.38	9.35	9.43	8.86
ALB222	2540±60	9.42	10.13	9.47	10.64	9.30	10.34	10.63	10.20	9.64	9.61	10.54	11.36	10.02
ALB301	2570±50	9.34	10.81	9.94	9.66	9.95	10.52	9.32	10.64	10.60	9.57	9.01	10.94	9.51
A1115	2588±28	10.20	9.22	8.96	10.52	9.95	10.78	10.38	**12.01**	10.96	11.07	9.61	10.65	10.36
UCT167	2695±45	6.60	8.95	8.69	9.48	9.01	9.24	8.84	9.50	9.21	8.72	**11.52**	8.93	8.99
UCT445	2720±60	10.61	11.38	9.68	10.33	9.81	10.71	11.02	9.42	11.06	11.19	**11.78**	10.20	9.63
SAM5049	2740±50	7.78	9.46	8.03	9.48	8.81	10.75	9.06	9.98	10.53	8.76	10.43	8.96	8.65
SAM5048	2780±60	9.98	10.19	8.99	10.78	9.63	9.64	10.22	**11.65**	**11.85**	10.13	10.29	10.75	8.68
UCT162	2880±50	7.47	10.25	9.18	9.82	10.63	10.32	9.90	10.76	9.43	9.03	10.51	9.86	10.75
SAM6147	2920±60	8.06	9.93	9.02	10.00	10.36	9.70	10.92	10.72	9.72	9.28	**11.50**	10.03	9.64
SAM6071	2935±32	9.11	10.52	8.97	10.11	10.26	10.35	10.94	10.32	10.81	9.55	9.83	9.32	9.12
SAM6317	2970±60	8.12	10.45	8.97	10.58	9.63	10.27	10.32	10.70	10.10	10.27	9.30	9.51	9.71
NMB1242	3030±26	8.12	10.16	8.37	10.51	8.76	9.62	9.69	9.52	9.96	9.51	10.09	9.83	9.20
NMB1273	3050±60	8.42	10.32	9.32	9.95	9.29	10.58	8.87	11.13	9.61	8.70	10.99	10.05	9.47

NMB1202	3140±50	8.98	8.66	9.30	8.49	9.40	10.55	10.07	10.70	**11.52**	9.83	10.53	9.91	9.59
SAM1145	3210±70	9.40	10.68	8.63	9.05	9.37	9.88	9.99	9.42	9.72	10.35	9.48	9.35	8.16
NMB4	3236±33	9.30	10.96	8.58	11.08	11.05	**11.95**	11.30	**11.77**	10.75	10.57	**11.90**	11.24	10.60
SAM6318	3310±60	8.50	9.44	8.40	9.83	9.17	9.96	9.29	10.04	9.49	8.62	10.60	7.76	8.75
SAM1879	3440±60	7.57	8.62	8.21	9.11	8.46	9.00	9.91	9.72	10.75	8.48	9.88	9.79	8.55
SAM31	3576±30	8.77	**11.72**	10.26	10.29	11.22	10.71	10.00	11.34	**11.72**	9.91	**11.93**	**11.59**	10.60
SAM4931	3750±60	8.83	9.95	8.70	10.20	10.18	10.21	9.37	10.74	9.61	9.93	11.38	10.95	9.47
SAM32	3754±35	8.89	10.88	8.97	11.29	10.09	10.91	9.84	10.72	9.41	11.02	9.68	11.10	9.18
A1124	4320±32	9.74	**11.60**	9.89	**11.72**	**11.41**	9.73	11.38	**12.33**	11.03	10.66	**11.45**	**11.88**	11.16
UCT112	4445±50	8.56	9.87	8.61	9.10	10.48	10.10	9.79	10.29	10.85	7.54	11.34	10.60	9.70
ALB131	4700±60	8.07	9.43	9.71	8.64	9.49	9.90	10.04	11.22	10.49	9.99	9.89	9.39	9.16
NMB1275	4850±60	7.53	10.03	7.58	9.95	9.08	9.75	9.63	10.22	8.98	9.25	9.65	9.23	7.53
SAM6272	5830±80	8.38	9.95	9.18	10.05	9.77	10.47	10.16	10.78	10.61	9.86	10.73	11.07	9.47
UCT180	6180±70	9.25	10.45	9.87	11.03	10.07	9.68	9.64	11.00	11.26	10.50	11.10	10.37	9.69
SAM4182	6811±36	9.38	9.65	9.46	9.86	10.95	10.99	10.76	11.13	**12.25**	9.38	**11.63**	10.84	8.75
SAM5055	6995±50	9.24	10.49	9.82	9.23	9.64	10.47	11.24	10.83	**12.04**	10.30	11.23	10.36	9.85
UCT156	10110±80	9.49	11.21	10.35	10.84	9.15	11.10	10.86	11.18	**11.53**	9.16	10.79	**11.44**	9.50
SAM4692	*ca*.12000	9.46	10.83	9.29	11.29	9.75	**11.41**	10.31	**11.77**	11.21	9.95	10.89	10.72	9.80

Table continued:

		SAM4901 1892±28	SAM6264 1950±60	SAM3053 1990±50	SAM5035b 2011±30	SAM1443 2050±50	UCT387 2055±40	SAM1142 2090±27	UCT220 2100±21	SAM4636 2130±45	SAM6313b 2140±29	SAM5082 2150±60	SAM1441 2170±60	UCT134 2210±40
UCT262	510±40													
NMB1207	560±50													
UCT583	560±45													
UCT157	587±28													
SAM4867	590±45													
SAM6020	620±30													
SAM5035a	620±35													
NMB1219	650±60													
NMB1338	650±35													
UCT114	650±40													
UCT83	680±40													
SAM1446	740±30													
SAM5032	765±25													
A2226	800±50													
A1154	905±25													
UCT70	920±40													
UCT60	950±50													
SAM6332	980±50													
UCT227	1000±50													
SAM1260	1137±27													
A2227	1150±50													
SAM4905	1210±50													
SAM4898	1226±26													
SAM6074	1360±40													
NMB1707	1394±24													
SAM6334	1400±50													
SAM4874	1426±29													
SAM6149	1440±70													
SAM5083	1490±50													
SAM6213	1558±27													
UCT109	1590±50													
NMB83	1590±40													
SAM320g	1707±27													
SAM4630	1775±80													
A1166	1818±27													

SAM6041a	1824±27													
A1152	1850±35													
UCT429	1870±35													
SAM1473	1880±60													
SAM4901	1892±28	0												
SAM6264	1950±60	8.93	0											
SAM3053	1990±50	10.12	8.65	0										
SAM5035b	2011±30	10.67	10.08	10.31	0									
SAM1443	2050±50	10.36	8.57	9.88	10.46	0								
UCT387	2055±40	9.20	8.50	10.29	10.42	9.62	0							
SAM1142	2090±27	10.38	8.81	8.67	10.07	9.52	9.55	0						
UCT220	2100±21	10.26	9.86	9.59	10.74	9.56	9.19	7.62	0					
SAM4636	2130±45	10.20	8.84	9.14	10.30	9.85	8.40	9.91	10.39	0				
SAM6313b	2140±29	9.63	9.21	9.86	10.21	9.87	9.97	8.93	9.91	8.79	0			
SAM5082	2150±60	10.07	8.20	8.22	9.05	9.60	9.39	8.77	9.40	8.94	9.04	0		
SAM1441	2170±60	8.72	7.51	9.59	9.95	9.53	8.31	8.97	9.28	9.47	10.31	8.67	0	
UCT134	2210±40	10.72	10.58	10.62	10.18	9.99	9.26	10.02	8.97	9.21	9.77	8.33	10.02	0
SAM4942	2220±45	9.04	8.25	9.44	10.53	10.46	10.14	9.70	9.89	8.93	9.10	9.26	9.74	9.24
A1114	2271±33	10.67	9.72	10.20	10.83	9.42	10.83	9.25	9.82	10.76	10.43	10.64	9.82	10.47
UCT107	2290±50	8.96	8.52	9.32	10.53	10.25	9.46	8.90	9.88	8.87	8.42	9.38	10.12	9.74
SAM6043	2295±28	10.07	9.72	9.62	**11.43**	10.09	10.10	9.32	9.57	9.66	9.76	8.94	8.97	10.53
SAM34	2310±25	8.85	8.83	9.80	9.17	9.99	9.62	10.17	9.89	8.77	9.25	9.32	10.47	9.87
SAM1146	2321±28	9.78	8.88	10.73	10.79	10.19	9.14	9.34	9.51	9.83	9.14	10.47	9.93	10.43
NMB82	2335±40	9.49	8.56	9.72	8.94	9.97	9.24	9.23	8.82	8.95	9.52	9.30	8.35	10.14
SAM4899	2440±60	9.18	8.18	9.48	10.26	9.95	8.34	9.03	8.95	8.44	8.29	9.36	8.18	8.96
ALB222	2540±60	10.80	8.28	8.45	10.58	9.23	9.46	8.95	9.91	10.13	9.60	9.35	7.72	9.84
ALB301	2570±50	11.22	8.68	10.57	11.06	10.54	9.46	8.53	9.75	10.28	10.58	9.93	9.53	10.77
A1115	2588±28	11.02	9.49	10.03	11.37	10.22	10.81	9.91	9.39	10.14	10.25	9.66	9.89	9.77
UCT167	2695±45	9.66	6.63	8.39	9.48	9.39	9.42	8.44	9.33	9.12	8.42	7.19	9.38	10.04
UCT445	2720±60	9.95	9.43	10.82	10.59	**11.47**	10.04	10.51	10.66	9.20	**11.83**	9.06	9.29	**11.94**
SAM5049	2740±50	9.63	8.37	8.68	8.70	9.62	8.27	8.15	8.36	8.97	8.80	8.34	9.40	8.73
SAM5048	2780±60	11.19	9.11	10.20	**11.54**	9.77	10.73	10.41	8.80	9.44	8.33	9.68	10.52	11.18
UCT162	2880±50	10.36	9.02	10.37	10.46	10.93	9.59	8.87	9.21	10.02	10.99	9.60	9.68	10.42
SAM6147	2920±60	9.41	7.78	9.70	9.71	9.60	8.20	8.70	9.17	9.66	9.18	9.02	8.00	10.71
SAM6071	2935±32	8.51	9.16	9.30	10.01	9.63	8.87	8.87	7.30	8.64	9.39	9.73	9.02	9.69
SAM6317	2970±60	10.05	9.03	9.26	10.40	9.14	9.55	9.68	9.00	8.99	8.88	9.78	9.81	10.12
NMB1242	3030±26	10.73	9.30	11.06	9.93	10.33	9.15	8.88	8.46	9.24	8.43	9.24	9.50	10.31
NMB1273	3050±60	10.67	7.61	8.92	10.18	7.63	8.85	8.92	9.65	7.56	8.48	8.14	9.27	9.82

NMB1202	3140±50	9.80	9.01	8.44	9.31	9.44	8.92	9.24	8.65	9.19	9.84	9.15	10.19	10.10
SAM1145	3210±70	10.22	7.92	10.13	11.09	9.02	10.12	8.71	10.29	9.64	9.21	8.41	9.60	10.14
NMB4	3236±33	10.26	9.45	**11.44**	10.20	9.76	9.70	11.08	9.71	10.82	11.11	10.02	9.99	10.62
SAM6318	3310±60	9.76	7.85	10.24	9.59	8.69	8.17	8.81	9.29	9.62	9.20	9.19	8.44	9.94
SAM1879	3440±60	9.54	7.93	9.14	9.95	9.76	8.14	8.93	8.29	8.34	8.60	9.07	9.10	9.34
SAM31	3576±30	9.64	9.24	9.82	**11.79**	11.30	9.65	11.12	10.17	10.29	9.30	10.36	10.80	**11.57**
SAM4931	3750±60	8.29	8.34	9.47	10.58	10.38	9.40	9.46	9.33	9.76	9.07	8.23	8.77	10.02
SAM32	3754±35	10.09	8.45	10.15	10.93	9.09	9.09	10.12	9.20	9.64	9.67	10.16	8.99	9.51
A1124	4320±32	**11.83**	10.90	10.71	**12.41**	**12.02**	10.43	10.29	**11.45**	9.31	10.52	10.86	11.09	**11.52**
UCT112	4445±50	9.00	8.83	9.35	10.48	8.56	8.82	8.85	8.43	9.80	9.13	9.66	8.85	10.22
ALB131	4700±60	9.92	8.83	9.09	10.08	10.24	7.68	9.31	8.84	9.01	8.43	9.34	10.08	9.29
NMB1275	4850±60	9.36	7.51	8.43	10.34	8.98	9.38	8.53	8.10	8.36	8.71	7.97	9.01	10.24
SAM6272	5830±80	10.64	8.39	10.98	10.55	10.14	8.83	9.04	9.48	9.91	9.31	9.82	9.58	10.48
UCT180	6180±70	9.41	8.97	9.92	11.09	10.87	9.63	9.70	9.56	10.21	8.69	9.37	9.36	10.04
SAM4182	6811±36	9.94	9.77	10.03	10.73	10.03	9.17	8.62	7.57	10.59	8.77	9.61	10.46	10.93
SAM5055	6995±50	10.01	9.27	10.05	10.43	10.46	9.22	9.48	9.41	9.95	9.87	9.42	9.46	9.69
UCT156	10110±80	10.64	9.52	9.42	11.14	10.39	9.94	10.53	8.95	10.00	9.97	9.58	10.63	10.85
SAM4692	*ca.*12000	10.60	10.12	10.84	11.32	10.97	10.68	10.60	9.28	10.63	10.30	10.15	11.18	10.66

Table continued:

		SAM4942 2220±45	A1114 2271±33	UCT107 2290±50	SAM6043 2295±28	SAM34 2310±25	SAM1146 2321±28	NMB82 2335±40	SAM4899 2440±60	ALB222 2540±60	ALB301 2570±50	A1115 2588±28	UCT167 2695±45	UCT445 2720±60
UCT262	510±40													
NMB1207	560±50													
UCT583	560±45													
UCT157	587±28													
SAM4867	590±45													
SAM6020	620±30													
SAM5035a	620±35													
NMB1219	650±60													
NMB1338	650±35													
UCT114	650±40													
UCT83	680±40													
SAM1446	740±30													
SAM5032	765±25													
A2226	800±50													
A1154	905±25													
UCT70	920±40													
UCT60	950±50													
SAM6332	980±50													
UCT227	1000±50													
SAM1260	1137±27													
A2227	1150±50													
SAM4905	1210±50													
SAM4898	1226±26													
SAM6074	1360±40													
NMB1707	1394±24													
SAM6334	1400±50													
SAM4874	1426±29													
SAM6149	1440±70													
SAM5083	1490±50													
SAM6213	1558±27													
UCT109	1590±50													
NMB83	1590±40													
SAM320g	1707±27													
SAM4630	1775±80													
A1166	1818±27													

SAM6041a	1824±27													
A1152	1850±35													
UCT429	1870±35													
SAM1473	1880±60													
SAM4901	1892±28													
SAM6264	1950±60													
SAM3053	1990±50													
SAM5035b	2011±30													
SAM1443	2050±50													
UCT387	2055±40													
SAM1142	2090±27													
UCT220	2100±21													
SAM4636	2130±45													
SAM6313b	2140±29													
SAM5082	2150±60													
SAM1441	2170±60													
UCT134	2210±40													
SAM4942	2220±45	0												
A1114	2271±33	10.86	0											
UCT107	2290±50	8.51	10.60	0										
SAM6043	2295±28	10.95	11.06	10.25	0									
SAM34	2310±25	9.98	9.81	8.71	9.94	0								
SAM1146	2321±28	9.99	8.45	8.94	10.46	8.91	0							
NMB82	2335±40	9.03	9.79	9.99	9.51	8.75	9.49	0						
SAM4899	2440±60	10.00	8.95	8.29	8.94	8.38	8.92	8.20	0					
ALB222	2540±60	8.42	10.07	9.82	9.92	10.81	9.64	8.74	9.68	0				
ALB301	2570±50	**11.41**	10.49	10.35	10.79	10.22	9.35	8.45	8.99	10.46	0			
A1115	2588±28	10.25	9.04	10.83	9.77	9.85	10.15	10.32	10.02	9.60	10.42	0		
UCT167	2695±45	7.30	9.87	8.97	10.16	7.55	8.99	9.48	8.57	8.88	10.17	10.23	0	
UCT445	2720±60	10.16	**11.58**	10.21	10.24	10.28	11.19	10.28	10.42	10.63	**11.51**	11.06	9.73	0
SAM5049	2740±50	9.32	10.52	7.41	9.92	8.00	9.42	7.62	9.03	9.08	8.78	8.98	8.31	10.72
SAM5048	2780±60	10.16	11.12	9.18	10.41	9.79	9.29	9.68	9.75	9.75	10.64	10.68	9.80	10.33
UCT162	2880±50	9.56	10.99	9.56	9.70	9.90	9.93	9.78	9.56	10.77	10.23	10.86	9.31	10.37
SAM6147	2920±60	9.44	9.59	8.66	10.15	8.45	9.08	9.00	8.99	8.61	10.60	10.88	8.28	9.80
SAM6071	2935±32	8.94	9.45	8.63	9.43	8.69	9.06	8.80	8.11	9.92	10.10	10.64	8.80	9.22
SAM6317	2970±60	9.46	10.10	9.20	9.60	9.31	8.65	9.26	9.39	9.86	10.43	9.83	8.50	10.76
NMB1242	3030±26	10.53	10.21	8.27	10.10	8.98	9.16	10.14	8.64	10.57	9.78	10.17	9.05	8.82
NMB1273	3050±60	8.91	9.33	8.20	9.96	9.58	9.02	9.54	8.10	8.59	9.24	10.67	8.20	9.90

NMB1202	3140±50	9.72	8.86	8.73	10.12	8.17	9.06	9.74	8.73	10.06	9.48	9.29	8.90	9.32
SAM1145	3210±70	10.44	9.21	8.53	8.33	9.11	8.10	9.12	8.20	9.67	9.20	9.70	8.74	9.34
NMB4	3236±33	**11.42**	11.04	10.90	11.10	10.00	10.66	9.05	8.48	10.77	11.09	11.34	10.11	11.18
SAM6318	3310±60	9.58	8.99	9.66	10.49	8.47	8.24	9.26	9.12	8.26	9.78	10.40	6.59	9.90
SAM1879	3440±60	9.06	9.92	8.63	8.84	8.73	7.87	8.39	8.37	8.92	9.56	9.94	8.02	9.54
SAM31	3576±30	10.97	11.39	10.28	11.27	10.59	10.08	10.63	8.79	10.96	**11.84**	**11.42**	9.85	11.21
SAM4931	3750±60	8.09	10.51	8.38	10.03	8.00	9.63	8.29	9.26	9.33	9.91	10.27	7.62	10.35
SAM32	3754±35	9.78	10.52	9.57	9.46	9.50	9.65	10.12	8.02	9.25	10.51	9.60	8.87	10.04
A1124	4320±32	**12.16**	11.12	10.95	11.30	11.26	**11.49**	10.90	9.61	10.63	11.10	**12.54**	10.89	**11.86**
UCT112	4445±50	10.40	10.10	8.70	9.67	9.73	10.88	9.98	8.69	10.20	9.88	9.94	9.58	10.69
ALB131	4700±60	9.00	9.87	8.39	10.32	8.29	8.49	9.51	7.37	8.86	9.97	10.00	7.98	10.55
NMB1275	4850±60	8.93	10.05	8.77	8.18	8.29	9.59	8.71	8.02	9.29	9.39	7.80	7.83	7.86
SAM6272	5830±80	9.96	10.80	10.61	10.32	9.61	9.84	10.01	8.90	9.93	9.31	9.51	8.67	10.59
UCT180	6180±70	8.87	9.49	10.07	**11.43**	10.67	9.62	9.91	8.95	10.81	10.55	10.79	8.45	10.46
SAM4182	6811±36	10.15	10.53	10.68	10.46	9.94	10.03	10.40	10.23	10.97	11.07	10.77	7.87	11.24
SAM5055	6995±50	10.10	**11.54**	9.26	9.27	9.43	9.19	10.71	9.70	9.40	10.90	10.55	9.01	10.53
UCT156	10110±80	9.98	10.16	10.01	10.48	11.10	10.10	10.02	9.46	9.61	10.24	11.14	9.28	11.07
SAM4692	*ca*.12000	9.39	11.22	9.82	11.05	9.46	9.39	9.54	10.37	9.64	9.82	11.04	8.79	**11.42**

Table continued:

		SAM5049 2740±50	SAM5048 2780±60	UCT162 2880±50	SAM6147 2920±60	SAM6071 2935±32	SAM6317 2970±60	NMB1242 3030±26	NMB1273 3050±60	NMB1202 3140±50	SAM1145 3210±70	NMB4 3236±33	SAM6318 3310±60	SAM1879 3440±60
UCT262	510±40													
NMB1207	560±50													
UCT583	560±45													
UCT157	587±28													
SAM4867	590±45													
SAM6020	620±30													
SAM5035a	620±35													
NMB1219	650±60													
NMB1338	650±35													
UCT114	650±40													
UCT83	680±40													
SAM1446	740±30													
SAM5032	765±25													
A2226	800±50													
A1154	905±25													
UCT70	920±40													
UCT60	950±50													
SAM6332	980±50													
UCT227	1000±50													
SAM1260	1137±27													
A2227	1150±50													
SAM4905	1210±50													
SAM4898	1226±26													
SAM6074	1360±40													
NMB1707	1394±24													
SAM6334	1400±50													
SAM4874	1426±29													
SAM6149	1440±70													
SAM5083	1490±50													
SAM6213	1558±27													
UCT109	1590±50													
NMB83	1590±40													
SAM320g	1707±27													
SAM4630	1775±80													
A1166	1818±27													

SAM6041a	1824±27								
A1152	1850±35								
UCT429	1870±35								
SAM1473	1880±60								
SAM4901	1892±28								
SAM6264	1950±60								
SAM3053	1990±50								
SAM5035b	2011±30								
SAM1443	2050±50								
UCT387	2055±40								
SAM1142	2090±27								
UCT220	2100±21								
SAM4636	2130±45								
SAM6313b	2140±29								
SAM5082	2150±60								
SAM1441	2170±60								
UCT134	2210±40								
SAM4942	2220±45								
A1114	2271±33								
UCT107	2290±50								
SAM6043	2295±28								
SAM34	2310±25								
SAM1146	2321±28								
NMB82	2335±40								
SAM4899	2440±60								
ALB222	2540±60								
ALB301	2570±50								
A1115	2588±28								
UCT167	2695±45								
UCT445	2720±60								
SAM5049	2740±50	0							
SAM5048	2780±60	9.49	0						
UCT162	2880±50	9.25	11.01	0					
SAM6147	2920±60	8.96	9.75	9.23	0				
SAM6071	2935±32	8.69	9.00	8.94	8.29	0			
SAM6317	2970±60	8.39	9.22	9.98	10.41	9.06	0		
NMB1242	3030±26	8.98	8.45	9.93	8.49	9.09	8.88	0	
NMB1273	3050±60	9.16	7.83	10.13	8.72	8.55	9.48	8.75	0

NMB1202	3140±50	8.04	8.98	9.21	8.78	7.62	9.17	9.11	7.78	0				
SAM1145	3210±70	8.73	8.82	10.69	9.61	9.62	8.61	9.21	8.68	9.27	0			
NMB4	3236±33	9.63	11.03	10.79	10.48	10.27	10.40	10.28	9.12	10.80	10.31	0		
SAM6318	3310±60	8.53	9.60	10.14	6.95	7.87	9.39	9.12	8.32	9.09	9.42	10.03	0	
SAM1879	3440±60	8.10	8.73	9.10	8.40	8.39	8.73	7.93	8.98	7.95	8.94	10.60	7.98	0
SAM31	3576±30	10.32	9.75	10.28	9.77	10.11	10.78	10.45	10.48	10.96	10.06	10.99	11.06	9.50
SAM4931	3750±60	7.96	9.87	9.25	8.45	8.59	9.51	9.89	9.15	9.50	9.39	10.50	8.95	8.64
SAM32	3754±35	9.42	9.67	10.51	10.66	8.92	8.74	9.21	8.84	9.45	8.90	10.71	9.34	8.47
A1124	4320±32	**11.54**	**11.70**	**11.53**	11.07	10.52	**11.57**	10.21	10.12	11.08	11.32	11.14	10.99	9.66
UCT112	4445±50	8.03	9.25	9.34	9.34	7.83	9.94	8.82	8.20	8.53	9.81	9.59	8.89	8.56
ALB131	4700±60	8.57	9.13	10.26	7.85	9.32	9.21	8.76	7.77	7.46	9.32	9.50	8.63	9.27
NMB1275	4850±60	8.21	8.39	8.04	9.16	7.92	8.49	8.44	8.61	8.10	8.49	9.38	8.94	9.03
SAM6272	5830±80	9.52	10.55	10.61	9.97	10.57	9.99	9.36	9.90	9.28	9.90	10.83	9.08	9.27
UCT180	6180±70	9.93	10.36	10.39	10.98	9.83	8.11	9.41	10.02	9.99	10.26	10.77	9.60	9.13
SAM4182	6811±36	8.56	10.58	10.97	9.59	9.12	10.40	9.44	10.70	9.55	10.49	11.26	9.23	8.12
SAM5055	6995±50	9.12	10.28	11.35	9.61	10.35	9.28	8.55	10.03	9.73	9.85	10.10	9.33	8.61
UCT156	10110±80	10.86	10.16	11.34	10.56	10.39	10.49	10.00	9.54	10.07	10.72	**11.45**	10.33	9.10
SAM4692	*ca.*12000	9.49	9.45	11.13	9.99	9.79	10.64	9.93	9.60	10.44	10.61	10.82	8.70	8.60

Table continued:

		SAM31 3576±30	SAM4931 3750±60	SAM32 3754±35	A1124 4320±32	UCT112 4445±50	ALB131 4700±60	NMB1275 4850±60	SAM6272 5830±80	UCT180 6180±70	SAM4182 6811±36	SAM5055 6995±50	UCT156 10110±80	SAM4692 *ca.*12000
UCT262	510±40													
NMB1207	560±50													
UCT583	560±45													
UCT157	587±28													
SAM4867	590±45													
SAM6020	620±30													
SAM5035a	620±35													
NMB1219	650±60													
NMB1338	650±35													
UCT114	650±40													
UCT83	680±40													
SAM1446	740±30													
SAM5032	765±25													
A2226	800±50													
A1154	905±25													
UCT70	920±40													
UCT60	950±50													
SAM6332	980±50													
UCT227	1000±50													
SAM1260	1137±27													
A2227	1150±50													
SAM4905	1210±50													
SAM4898	1226±26													
SAM6074	1360±40													
NMB1707	1394±24													
SAM6334	1400±50													
SAM4874	1426±29													
SAM6149	1440±70													
SAM5083	1490±50													
SAM6213	1558±27													
UCT109	1590±50													
NMB83	1590±40													
SAM320g	1707±27													
SAM4630	1775±80													
A1166	1818±27													

SAM6041a	1824±27
A1152	1850±35
UCT429	1870±35
SAM1473	1880±60
SAM4901	1892±28
SAM6264	1950±60
SAM3053	1990±50
SAM5035b	2011±30
SAM1443	2050±50
UCT387	2055±40
SAM1142	2090±27
UCT220	2100±21
SAM4636	2130±45
SAM6313b	2140±29
SAM5082	2150±60
SAM1441	2170±60
UCT134	2210±40
SAM4942	2220±45
A1114	2271±33
UCT107	2290±50
SAM6043	2295±28
SAM34	2310±25
SAM1146	2321±28
NMB82	2335±40
SAM4899	2440±60
ALB222	2540±60
ALB301	2570±50
A1115	2588±28
UCT167	2695±45
UCT445	2720±60
SAM5049	2740±50
SAM5048	2780±60
UCT162	2880±50
SAM6147	2920±60
SAM6071	2935±32
SAM6317	2970±60
NMB1242	3030±26
NMB1273	3050±60

NMB1202	3140±50													
SAM1145	3210±70													
NMB4	3236±33													
SAM6318	3310±60													
SAM1879	3440±60													
SAM31	3576±30	0												
SAM4931	3750±60	10.05	0											
SAM32	3754±35	10.81	9.34	0										
A1124	4320±32	**12.14**	**12.15**	11.25	0									
UCT112	4445±50	9.17	9.03	9.86	**11.43**	0								
ALB131	4700±60	9.79	9.82	9.36	10.22	10.35	0							
NMB1275	4850±60	9.57	9.53	8.42	10.38	8.99	8.37	0						
SAM6272	5830±80	10.82	10.60	9.92	**11.91**	10.50	9.03	8.07	0					
UCT180	6180±70	10.65	9.86	10.03	11.07	10.00	9.79	8.57	9.18	0				
SAM4182	6811±36	10.26	9.48	9.96	11.08	9.60	9.55	9.07	9.85	9.18	0			
SAM5055	6995±50	**11.75**	10.10	10.96	11.39	10.23	8.40	9.60	10.20	9.98	9.28	0		
UCT156	10110±80	10.28	10.58	10.27	**11.77**	10.86	8.88	9.65	9.83	10.47	9.83	10.25	0	
SAM4692	*ca.*12000	11.27	7.68	10.43	**11.85**	10.73	9.83	10.39	9.77	10.98	10.00	10.36	9.24	0

Appendix 4: Mahalanobis distances (D) between all female crania.

		A1153 636±26	SAM4180 688±27	UCT582 740±40	SAM5012 812±26	A1117 1060±50	SAM1247 1180±50	ALB244(1) 1180±50	UCT94 1270±40	SAM4314 1319±25	SAM6075 1330±40	SAM4669 1333±25	UCT75 1340±40	SAM4920a 1364±32
A1153	636±26	0												
SAM4180	688±27	**11.65**	0											
UCT582	740±40	8.60	10.55	0										
SAM5012	812±26	8.56	10.39	8.11	0									
A1117	1060±50	9.02	10.47	8.08	9.00	0								
SAM1247	1180±50	9.50	**11.63**	10.30	9.44	10.01	0							
ALB244(1)	1180±50	11.30	11.20	9.77	9.90	8.91	10.06	0						
UCT94	1270±40	9.59	10.09	8.92	8.82	9.29	9.44	8.69	0					
SAM4314	1319±25	8.70	10.80	7.97	8.61	7.71	9.65	9.30	9.22	0				
SAM6075	1330±40	9.65	9.80	8.87	8.87	8.98	9.76	9.65	6.97	9.90	0			
SAM4669	1333±25	11.19	**11.99**	11.17	10.44	10.70	10.40	**11.54**	10.02	11.24	9.56	0		
UCT75	1340±40	10.49	10.44	9.92	9.07	10.15	10.27	10.43	9.42	9.74	9.82	11.10	0	
SAM4920a	1364±32	9.85	10.40	9.88	9.11	10.31	**11.54**	10.69	9.31	10.18	9.26	10.16	**11.42**	0
SAM5034	1390±40	9.30	10.02	9.13	7.93	9.35	9.41	10.20	8.37	8.51	8.91	10.87	9.99	8.95
NMB5	1423±26	8.82	9.35	8.65	8.67	8.42	9.71	9.20	8.64	10.28	6.83	9.99	10.37	8.98
SAM4790	1610±150	9.38	10.39	10.07	9.71	10.39	**11.77**	10.60	9.46	10.01	8.58	10.86	9.54	11.28
ALB323	1620±35	10.21	11.28	9.87	8.63	10.54	10.55	10.99	10.21	8.29	9.24	**11.73**	8.94	9.88
UCT55	1680±40	9.84	11.22	9.79	9.89	9.14	9.48	9.23	8.78	9.35	9.43	**11.77**	10.46	11.04
SAM4659	1815±29	9.68	10.98	8.07	8.55	8.99	10.11	10.05	8.75	8.71	9.49	10.39	10.06	10.02
A1127	1891±29	9.52	**11.49**	9.14	9.14	9.36	9.60	9.13	9.13	9.99	9.78	**11.47**	10.37	9.14
UCT120	1960±50	8.40	9.42	8.98	8.02	9.23	9.69	10.26	8.51	9.35	8.74	10.73	8.11	10.30
SAM5041	2010±50	9.80	9.51	8.16	9.02	8.91	10.02	8.73	8.17	7.40	8.67	10.51	9.88	10.34
SAM6260a	2120±60	9.58	11.26	8.03	8.80	8.75	11.34	9.39	9.21	8.81	9.35	**11.43**	10.15	9.83
UCT78	2145±40	9.03	9.12	7.07	8.04	8.02	8.85	8.67	6.94	7.64	8.15	9.65	9.56	8.69
SAM278g	2158±28	8.21	10.46	7.81	8.15	9.47	10.09	9.93	7.64	8.19	8.79	10.82	9.38	9.63
SAM6313a	2161±30	9.84	9.69	8.81	8.04	9.32	10.03	9.63	8.30	9.20	7.74	10.64	9.49	9.36
NMB1203	2180±50	9.80	**11.68**	9.37	8.52	9.62	10.33	9.21	10.05	9.97	8.92	11.13	9.81	9.97
NMB1204	2210±35	9.03	9.30	7.62	9.08	9.13	9.91	9.25	7.88	8.59	8.75	10.49	9.78	9.49
UCT436	2240±60	10.23	10.93	8.71	9.44	10.00	10.32	8.87	8.49	8.70	10.11	10.54	10.45	9.89
SAM4301	2250±30	8.94	10.28	8.31	6.92	9.13	9.63	9.08	8.25	8.69	8.08	10.21	8.53	9.01
SAM4312	2260±170	10.34	11.31	9.61	9.52	9.54	10.38	**11.81**	8.48	9.31	9.50	11.28	10.93	10.17
SAM4299	2294±29	10.29	10.47	9.93	8.21	8.25	10.86	8.45	8.28	8.79	9.25	10.76	9.33	9.75
SAM4300	2304±29	9.51	10.12	8.15	9.22	8.64	10.04	9.49	8.68	9.33	8.40	10.02	9.25	9.54